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THE QUARTERLY REVIEW of BIOLOGY

QUANTITATIVE LAWS IN METABOLISM AND GROWTH

By LUDWIG VON BERTALANFFY

Biological Research, Mt. Sinai Hospital, and University of Southern California, Los Angeles

INTRODUCTION

THE work reviewed in this paper is aimed at establishing connections between two fundamental aspects of living organisms, their metabolism and growth. What we call growth of even a simple organism is a tremendously complex phenomenon from the biochemical, physiological, cytological, and morphological viewpoints. There are, however, certain aspects that are amenable to quantitative analysis, and such an approach appears to lead to some insight into the connections between metabolism and growth, and to some answer to the seemingly trivial, but in fact hardly explored question, "Why does an organism grow at all, and why, after a certain time, does its growth come to a stop?"

QUANTITATIVE RELATIONS BETWEEN BODY SIZE AND METABOLIC RATE

In order to begin this investigation, it may be emphasized that, in many physiological activities, the absolute size of the body is a most important factor determining the rate of processes. Whether we take total metabolism, heart or respiratory rate, the chemical composition of the organism, excretion, or the enzyme content of the cells—we always will find that they characteristically vary with body size, this being true even though the the organisms compared in such respects show a tremendous diversity in their anatomy, physiological mechanisms, adaptations to certain environments, and so forth (cf. Adolph, 1949). To give just one example: pulse rate in mammals closely corresponds to the ¾ power of body weight over seven orders of magnitude, from a dwarf bat weighing some four grams, to an elephant of 2000 kilograms, in spite of the fact that the animals under comparison belong to different orders, and are adapted to all sorts of climate and ways of living (Fig. 1).

The relation between metabolic rate and body size belongs to the classical topics of physiology. It goes back over more than a hundred years to the time when Sarrus and Rameaux, Bergmann and Leuckart, and Richet noticed that weight-specific metabolic rate, that is, the intensity of metabolism as measured by oxygen consumption or calorie production per kilogram of body weight, decreases with increasing body size. A classical example is provided by Rubner's experiments with dogs of different size (Table 1). It appears that metabolic rate per kilogram decreases. If, however, metabolism is calculated per unit of body surface, approximately constant values appear. The comparison of metabolic rates in mammals led Rubner to the contention that warm-blooded animals produce daily about 1000 Cal. per square meter of body surface. This is the origin of the famous *surface rule*, which was explained by Rubner in terms of homeothermy. All warm-blooded animals heat their bodies to a temperature of ca. 37°C. Heat output takes place through the body surface. Hence, the same number of calories must be produced per unit surface in order to maintain the body temperature constant.

There are, however, considerable difficulties

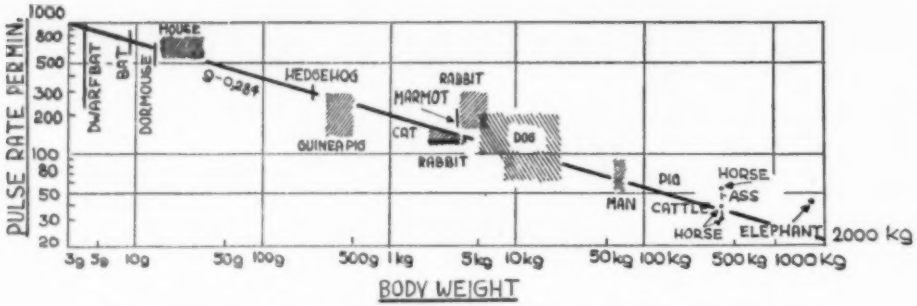

FIG. 1. ALLOMETRIC DEPENDENCE OF PULSE FREQUENCY ON BODY WEIGHT IN MAMMALS

It may be assumed that the volume of blood transported per minute is proportional to the basal metabolic rate, as the oxygen consumed must be transported by the blood. This volume is equal to stroke volume (S) × pulse frequency (F). In a rough first approximation, S may be taken as proportional to body weight (W). The basal metabolic rate follows interspecifically, in the series of mammals, the $W^{\frac{3}{4}}$ rule. Hence:

$$S.F. = CW^{\frac{3}{4}}, \text{ and}$$

$$F = \frac{C'W^{\frac{3}{4}}}{W} = C'W^{-\frac{1}{4}}$$

The figure shows that the allometry constant of pulse frequency, $\alpha = -.28$. Notwithstanding the gross oversimplification which neglects anatomical, physiological, ecological, and other differences, absolute body size is the dominating factor in the control of pulse frequency, in a range from the dwarf bat (4 g. body weight) to the elephant (2000 kg.). Modified after Bertalanffy (1951a).

TABLE 1

Metabolism in dogs
After Rubner (1902).

Weight in kg.	Cal. production per kg.	Cal. production per sq. m. body surface
3.1	85.8	1909
6.5	61.2	1073
11.0	57.3	1191
17.7	45.3	1047
19.2	44.6	1141
23.7	40.2	1082
30.4	34.8	984

in measuring the outer surfaces of animals exactly, but a simple mathematical device can be applied. If two bodies are reasonably similar in shape, their surfaces can be expressed as a $\frac{2}{3}$ power of weight, since the cubic root of the volume or weight is a linear dimension, and therefore its square has the dimension of a surface. Hence, the surface areas of geometrically similar bodies can be obtained by multiplying the $\frac{2}{3}$ power of the weight by a suitable constant. This is seen in the well-known formula of Meeh:

$$S = bW^{\frac{2}{3}} \qquad (1)$$

The surface rule of metabolism accordingly states that the basal metabolic rate is proportional to the $\frac{2}{3}$ power of the weight. In the case of man, the determination of the basal metabolism is a clinical routine, in order to diagnose thyroid disorders and the like. Here the somewhat more complicated Dubois formula is applied. Dimensionally, however, the Dubois formula is identical with the surface rule. The Dubois formula is: $S = kW^{0.425} \times L^{0.725}$. As, presupposing geometrical similarity, length $L = cW^{\frac{1}{3}}$, this can be written: $S = kW^{0.425}.\ cW^{0.725(0.33)} = bW^{\frac{2}{3}}$.

The relation between metabolic rate and body size can be studied either intraspecifically, i.e., by comparing animals of the same species and different body size, or interspecifically, i.e., by comparing adult animals of different species. We are at present mainly concerned with intraspecific comparison.

A grave objection can be raised against the surface rule as found in textbooks of physiology. In considering the quantitative relation between metabolic rate and body size, homeothermic vertebrates and, in particular, mammals are almost solely taken into account (e.g., Brody, 1945; Kleiber, 1947; Krebs, 1950). However, the case of mammals is by no means simple but rather

is intricate. Moreover, as we shall see presently, many familiar conclusions and explanatory hypotheses fall flat if not only mammals but also poikilothermic vertebrates and invertebrates are taken into consideration. It is therefore necessary to consider the problem on the broader basis of comparative physiology. A considerable part of this work has been carried through in the author's laboratories.

In order to understand these results, one more mathematical formula is necessary. The dependence of the metabolic rate of an animal on body size can be expressed in the equation:

$$M = bW^{\alpha}, \qquad (2)$$

where M is the metabolic rate per unit time, W the body weight, and α and b are constants. This is a special case of the so-called *allometric formula* (Huxley, 1932) which expresses the dependence on body size for an enormous amount of morphological, biochemical, physiological, and evolutionary data. This formula can further be written in the following way:

$$\log M = \log b + \alpha \log W \qquad (3)$$

That is to say, if metabolic rate is plotted against body weight double-logarithmically, we obtain a straight line the slope of which indicates the constant α. If $\alpha = \frac{2}{3}$, the metabolic rate follows the surface rule. If $\alpha = 1$ or the slope is 45°, the metabolic rate is proportional to weight. With $1 > \alpha > \frac{2}{3}$, an intermediary case obtains.

If weight-specific values are taken, that is, if metabolic rate per unit weight is plotted instead of that of the total animal, the equation becomes:

$$\frac{M}{W} = bW^{\alpha-1} \qquad (4)$$

Correspondingly, weight-specific metabolic rates, as a general rule, decrease with increasing weight, and the slope of the logarithmic plot is negative.

After these preliminaries, we can summarize the experimental results in the following way (Bertalanffy, 1941b, et seq.):

1. The surface rule also holds for poikilothermic vertebrates and certain invertebrates. The rule is, therefore, of a wide application; but the explanation given by Rubner is too restricted, for in poikilothermic animals there is no thermoregulation, and thus the latter cannot be the basic factor in the relation between body size and metabolic rate.

2. On the other hand, there are many classes of animals in which the surface rule does not hold.

TABLE 2

CO_2 production of Armadillidium pallasii
(Temperature 21°C.)
After Müller (1943b).

Weight in mg.	15	33	50	100	160
Cmm. CO_2/hr.	3.0	5.2	7.2	11.2	15.2
Per g./hr.	200	174	144	112	94
Per unit surface ($W^{\frac{1}{3}}$)/hr.	48.5	54.2	53.0	49.8	51.6

3. Thus we come to the statement that several metabolic types exist with respect to the relation between metabolic rate and body size.

In view of what was said previously, *three metabolic types*, that is, three different ways of dependence of the metabolic rate on body size can be distinguished, this classification applying, as was emphasized, to intraspecific allometry, that is, to individuals of different sizes or to growing animals within one species.

In the *first type*, metabolic rate is proportional to a surface or the $\frac{2}{3}$ power of the weight. Representatives of this type include fishes but also certain invertebrates, such as crustaceans, clams, and ascaris. Table 2 presents one example, the metabolic rate in the sowbug, *Armadillidium*. As can be seen, its oxygen consumption per unit weight decreases with increasing body size, but remains constant per unit surface. Subsequently it will be seen that sowbug and company reveal quite a bit about human growth as a central problem of physiology.

The *second type* is quite different. Here the metabolic rate is proportional not to surface area, but to weight itself, so oxygen consumption in an animal of double size is simply doubled, in an animal four times as large is quadrupled, etc. Direct proportionality of metabolic rate to weight is found in growing insect larvae and hemimetabolous insects, as well as interspecifically, in comparing imagos of different related species. Table 3 shows metabolic rates in the walking stick, *Dixippus morosus*. Oxygen consumption per gram and hour appears to be constant over a wide range, covering all body sizes and the entire development. Other groups belonging to this type are land snails of the family Helicidae, intraspecifically as well as interspecifically, and annelids such as the earthworm.

Finally, in the *third type* metabolic rates are

TABLE 3

Oxygen consumption of Dixippus morosus
(Temperature 20°C.)
After Müller (1943a).

Weight in mg.	8	130	250	450	630	850
Cmm. O_2/hr.	2.0	30.6	60.7	113.2	154.8	206.6
Per g./hr.	250	236	243	252	245	242

TABLE 4

Oxygen consumption of Planorbis sp.
(Temperature 23°C.)
After Bertalanffy and Müller (1943).

Weight in mg.	30–35	58–62	90–100	140	190–200
Cmm. O_2/hr.	2.3	3.9	5.4	7.3	9.5
Per g./hr.	69	65	56	52	48
Per unit surface ($W^{\frac{2}{3}}$)/hr.	22.9	25.1	26.1	27.0	28.2

intermediate between proportionality to weight and proportionality to surface area. To this type belong such pond snails as *Planorbis* and *Lymnaea* and flatworms like *Planaria*. Table 4 gives data for the ramshorn snail, and shows that its metabolic rate decreases with respect to its weight, but increases with respect to its surface area.

The relations mentioned are typical and characteristic of the species concerned. Table 5 gives a survey of available observations. A few minor discrepancies need elucidation, but in general it can be said that the "metabolic type," i.e., the relation of metabolic rate to body size, is a physiological characteristic of the species or group of species concerned.

INTERPRETATIONS OF THE SIZE DEPENDENCE OF METABOLISM

We now come to the question, what is at the basis of the relation between metabolic rate and body size and, in particular, of its most familiar form, the surface rule? (Cf. Kleiber, 1947; Bertalanffy, 1951a; Bertalanffy and Pirozynski, 1953; with further references). We must admit that we do not know. What can be shown, however, is that the explanations usually given are insufficient.

There seems to be, first, the alternative whether the dependence of metabolic rate on body size is based upon *cellular* or upon *organismic factors*. That is to say, the decrease of metabolic rate with increasing body size may be due to intrinsic differences in the metabolism of the cells of smaller and larger individuals, in which case it should also be found in the respiration of tissues taken out of the organism; or else, it may be regulated by factors present and active only in the organism as a whole. Let us start with the organismic hypotheses.

The most familiar one has already been mentioned, namely, *thermoregulation*. There is no doubt that energy expense for thermoregulation forms a considerable part of the total metabolism in homeothermic animals. However, this explanation cannot be general since the surface rule also applies, and in fact is more accurately established, in cold-blooded vertebrates and even in certain invertebrates where there is no thermoregulation.

Another interpretation assumes that the surface rule is based upon the *anatomy and physiology of the circulatory system*. The supply of oxygen and nutritive materials to the tissues is naturally a function of the intensity of the blood current. The latter depends on factors such as the size and stroke volume of the heart, the frequency of heart beat, the diameter of the blood vessels, the degree of capillarization, and the like. As has already been indicated, there are rather strict quantitative relations between body size, metabolic rate, and pulse rate. Thus, in interspecific comparison "from the mouse to the elephant", pulse rate decreases approximately proportional to the ¾ power of the weight (Fig. 1). So does basal metabolic rate in the interspecific comparison of mammals, if adult specimens of corresponding species are plotted (Brody, 1945; Kleiber, 1947). However, hemodynamics cannot offer a general explanation. Remember, for example, the clams, where the circulatory system is completely different from that found in vertebrates, or recall ascaris, which has no blood circulation at all—animals whose metabolic rate nevertheless follows the surface rule.

Recent investigations of the Ludwig laboratory (Ludwig, 1956; Kienle and Ludwig, 1956; Sattel, 1956) give some support to the hypothesis proposed by Ludwig and by Bertalanffy (1951a, p. 252f.) that the "metabolic types" are connected with *types of respiratory apparatus*. Gill-breathing animals appear to follow the surface rule; hence its validity in fish and certain inanimate classes. On the other hand, the surface of tracheas in insect larvae develops proportional to body volume, as was shown by Sattel (1956) in *Bombyx mori*; hence the proportionality of metabolic rate to weight.

TABLE 5

Relation between metabolic rate and body size

Species	Reference	Respiration proportional to $W^{2/3}$ (surface), W (weight) or intermediate
PLATYHELMINTHES		
Dugesia gonocephala	Bertalanffy and Müller, 1943	Intermediate
NEMATHELMINTHES		
Ascaris lumbricoides	Krüger, 1940	Surface
ANNELIDA		
Lumbricus sp.	Müller, 1943b	Weight
Eisenia foetida	Krüger, 1952	Surface?
MOLLUSCA		
Lamellibranchiata		
Anodonta cygnaea	Weinland, 1919	Surface
Dreissensia polymorpha	Ludwig and Krywienczyk, 1950	Surface
Prosobranchia		
Lithoglyphus, Paludina fasciata and P. vivipara	Krywienczyk, 1952a	Surface
Pulmonata		
Lymnaea stagnalis	Bertalanffy and Müller, 1943	Intermediate
Lymnaea stagnalis	Füsser and Krüger, 1951	Intermediate
Lymnaea auricularia	Krywienczyk, 1952b	Weight?
Planorbis sp.	Bertalanffy and Müller, 1943	Intermediate
Planorbis corneus	Füsser and Krüger, 1951	Intermediate
Planorbis corneus	Krywienczyk, 1952b	Intermediate
Isidora proteus	Krywienczyk, 1952b	Intermediate
Pulmonata and Operculata, 15 species intra-and interspecific	v. Brand, Nolan and Mann, 1948	Surface (high temperature [30°C.]?)
Helicidae		
Helix, Chilotrema, and Cepaea (interspecific)	Liebsch, 1929	Weight
Cepaea vindobonensis	Bertalanffy and Müller, 1943	Weight
CRUSTACEA		
Branchiopoda		
Daphnia pulex	Jančařík, 1948	Surface
Artemia salina	Bertalanffy and Krywienczyk, 1953	Surface
Isopoda		
Asellus aquaticus	Müller, 1943b	Surface
Asellus aquaticus	Will, 1952	Surface
Armadillidium pallasi	Müller, 1943b	Surface
Porcellio scaber	Will, 1952	Intermediate
Oniscus asellus	Will, 1952	Surface
Ligia oceanica	Ellenby, 1951	Probably surface
Decapoda		
Astacus astacus	Kalmus, 1930	Surface?
Potamobius torrentium	Wolsky, 1934	Weight?
Pugettia producta	Weymouth et al., 1944	Intermediate
Homarus vulgaris	Thomas, 1954	Surface
INSECTA		
Hemimetabola		
Dixippus morosus	Müller, 1943a	Weight
Holometabola		
Various species, intra- and interspecific	Kittel, 1941	Weight
Tenebrio molitor	Bertalanffy and Müller, 1943	Weight
PISCES		
Lebistes reticulatus	Bertalanffy and Müller, 1943	Surface
Various species (*Scorpaena, Abramis, Cyprinus*, etc.)	Jost, 1928	Surface
REPTILIA		
Lacerta	Kramer, 1934	Surface

Intermediate cases would result from the presence of two types of respiratory apparatus.

Still another explanation of the surface rule is based upon *anatomical or chemical changes* in composition with increasing body size. "Metabolically active" organs such as the viscera, the brain, etc., are relatively larger in small as compared to large animals. So it can be assumed that they consume relatively more oxygen and are responsible for the higher weight-specific metabolic rate in smaller organisms. However, the relative growth of inner organs is very different from one organ to the other, and so it is improbable that it can yield the simple relation of the surface rule of metabolism (cf. Bertalanffy, 1951a). A quantitative estimate (Bertalanffy and Pirozynski, 1953) shows that this factor is not sufficient to account for the actual variations of basal metabolic rate.

Now we come to the interpretations in terms of intracellular factors. This amounts to saying that the decrease of weight-specific metabolic rate with increasing size, as expressed in the surface rule, is due to a corresponding decrease in the *respiration of tissues*. Tissue respiration is measured as Q_{O_2}, that is, μl O_2/mg. dry weight/hr., as determined with the Warburg apparatus. A considerable amount of work has recently been done along these lines, partly stimulated by our own work now to be presented, just as we may also say that the interest in comparative metabolism as classified in the metabolic types mentioned has been stimulated by the investigations on growth laws to be explained hereafter. The question of the size dependence of tissue respiration is a controversial one, but the statements to follow appear to be a fair presentation of the case.

In interspecific comparison of mammalian species of different sizes, ranging from the mouse to the horse, a decrease of Q_{O_2} with increasing body size is generally found, as a number of observers have established (Kleiber, 1941; Weymouth, Field, and Kleiber, 1942; Krebs, 1950; Martin and Fuhrmann, 1955). This decrease, however, is not parallel in the various organs and, as a general rule, is less than would correspond to the surface rule or the $\frac{3}{4}$ power rule of metabolism. In a corresponding way, a decrease with increasing body size was found in enzymatic systems connected with respiration, such as in the concentration of glutathione (Gregory and Goss, 1933; Patrušev, 1937), of cytochrome c (Rosenthal and Drabkin, 1943), of cytochrome oxidase (Kunkel and Campbell, 1952), of succinodehydrase and malicodehydrase (Fried and Tipton, 1953).

The picture, however, is different in intraspecific comparisons, as between rat tissues from animals of different body size and age. Seven main organs of the rat have been investigated by Bertalanffy and Pirozynski (1951, 1953), and skeletal musculature, which is particularly important because it forms a high percentage of body mass, was studied by Bertalanffy and Estwick (1953). As Fig. 2 illustrates, no significant decline of average Q_{O_2} with increasing body size is found in brain, lung, and kidney; a slight decline in skeletal muscle, liver, and heart; and a marked decline in the diaphragm. So there is no systematic decrease of Q_{O_2} in the various organs consistent with, and responsible for the decrease of the weight-specific metabolic rate with increasing body size. These results have been essentially confirmed by other workers and with other materials: in growing chicken by Crandall and Smith (1952), in the heart muscle of the guinea pig by Wollenberger and Jehl (1952), in the teleost brain by Vernberg and Gray (1953), and in rat testes by Homma (1953). Similarly, Fried and Tipton (1953) did not find a decrease in the content of respiratory enzymes.

From this it would appear that genetic, and hence species-specific, differences in the enzymatic activity and Q_{O_2} of tissues are found in interspecific comparisons. Differences, however, in animals of the same species and different weight are irregular with respect to the various tissues or are absent.

So we have to assume factors which, within the intact organism, regulate the respiration of the tissues, the sum total of which is the metabolism of the entire animal, but which do not show up in the isolated tissue used for Warburg determination (Bertalanffy and Pirozynski, 1951, Schmidt-Nielsen, Bertalanffy, and Pirozynski, 1951). We have already said that the organismic factors usually contemplated do not offer a satisfactory explanation. What one may expect can be illustrated by the action of thyroxin. It is easy to induce an increase of metabolism by injection of thyroxin into the animal in vivo; but in spite of many efforts made, nobody has been able to reproduce satisfactorily this effect by an administration of thyroxin to a tissue in vitro. On the other hand, chronic hormonal conditions are manifested by significant changes of the tissue Q_{O_2}, as has been shown with tissues from

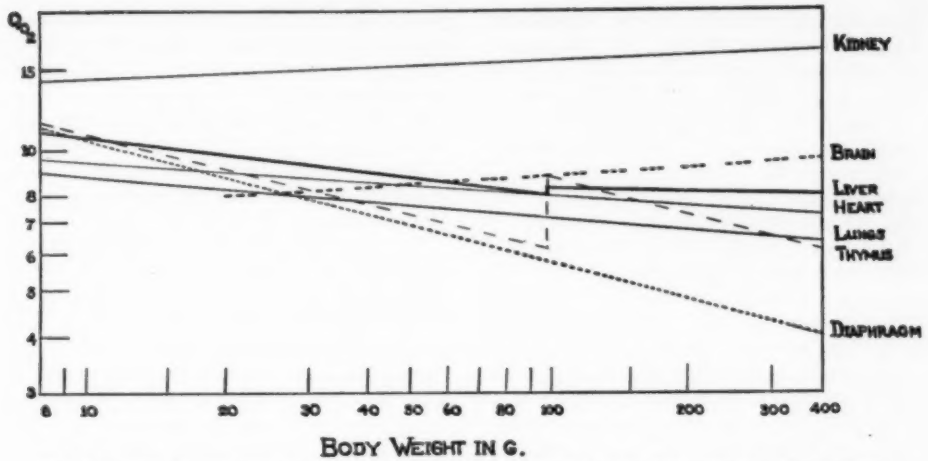

FIG. 2. TISSUE RESPIRATION OF VARIOUS ORGANS OF THE WHITE RAT IN RELATION TO BODY WEIGHT

Q_{O_2} = μl. O_2/mg. dry wt./hr.

Only regression lines are shown; for individual data and statistical evaluation cf. the original paper. After Bertalanffy and Pirozynski (1953).

hypophysectomized animals and in pituitary dwarf mice, which lack somatotrophin (Bertalanffy and Estwick, 1954).

The writer does not feel happy about this state of affairs, and the situation would be much more satisfactory if a straightforward relation between the decrease of the weight-specific metabolic rate and the tissue respiration could be found. Indeed, the Ottawa study was started with this expectation, which, unfortunately, was not borne out by the facts.

The explanation of the surface rule and of the size-dependence of metabolism in general thus remains rather unsatisfactory. We have, at present, to take the metabolic type, in the sense defined, as an empirical datum of the species concerned. However, even this cautious attitude leads to certain remarkable inferences with respect to the problem of growth.

METABOLIC TYPES AND GROWTH TYPES

It has already been stated that, among the various animal classes, so-called metabolic types can be distinguished by virtue of the relation between the metabolic rate and the body size. Now as there are different metabolic types, there are also different *growth types* which are distinguished by the course of growth as expressed in the growth curves of the several species. It appears that we have been successful in establishing a definite and strict connection between metabolic types and growth types, in consequence of a general theory of growth which establishes rational quantitative laws of growth and indicates the physiological mechanism upon which growth is based.

Let us start with a rather obvious deliberation, first indicated by Pütter (1920). Animal growth can be considered a result of a counteraction of synthesis and destruction, of the anabolism and catabolism of the building materials of the body. There will be growth so long as building up prevails over breaking down; the organism reaches a steady state if and when both processes are equal. We may express this in a general formula:

$$dW/dt = \eta W^m - \kappa W^n. \qquad (5)$$

In words: The change of body weight W is given by the difference between the processes of building up and breaking down; η and κ are constants of anabolism and catabolism respectively, and the exponents m and n indicate that the latter are proportional to some power of the body weight W.

Obviously the growth of any organism is of an enormous complexity, whether we consider it

from a biochemical, physiological, morphological, or any other aspect. However, the justification of an overall formula and the simple model it implies lies in the following. Our equation states that the gross result of synthetic and degradative processes within the organism follows the law of allometry, that is, that the rate of these processes can be expressed as a power function of body mass. But this assumption is justified, because at least in a first approximation the rate of all physiological processes hitherto investigated can be expressed in allometric or power formulas (Adolph, 1949). The intrinsic complexity of the phenomenon concerned does not preclude it from following such a simple, general law. Remember, for example, what has been found in the dependence of the basal or resting metabolism of the intact animal. Of course, what is called the basal metabolic rate is, in fact, the outcome of innumerable and to a large extent unknown processes of intermediary metabolism. Not only this, but the growing organism undergoes changes at the biochemical, physiological, cellular, and morphological levels. Nevertheless, we can state quite definitely that a certain organism obeys, let us say, the surface rule; that is, that the rate of metabolism of the entire animal, whatever its size or developmental age, can be expressed as a function of the $\frac{2}{3}$ power of its respective body weight.

We have now more closely to define the processes appearing in our basic equation. The catabolic processes mean, of course, the continuous loss of building material as it takes place in any living organism. Biochemically, this means the turnover of building materials and particularly of proteins, as demonstrated by the isotope techniques. Cytologically, it means the renewal of cells, as found in many tissues and organs, often at an unexpectedly high rate (cf. Leblond and Stevens, 1948; Storey and Leblond, 1951; F. D. Bertalanffy and Leblond, 1953; Leblond and Walker, 1956; a table of the rates of cell renewal as found by the Leblond school is given in Bertalanffy, 1957). The isotope and other techniques have shown that the animal organism maintains itself in a so-called dynamic or steady state (Schoenheimer, 1947), chemical components as well as cells being continually worn out or degraded, and on the other hand being replaced by way of resynthesis and the formation of new cells. So far as the rate of catabolism is concerned, we may assume, as a first approximation and based upon various physiological facts (cf. Bertalanffy, 1951a), that it is directly proportional to weight. On the other hand, mathematical considerations (Bertalanffy, 1941b) show that our basic equation is rather insensitive to smaller deviations of the exponent n from unity. So we may put, without any considerable loss of generality, the exponent n equal to 1. This makes the solution of our basic equation much easier.

The solution of equation 5 ($n = 1$) is (Bertalanffy, 1941b):

$$W = \left\{\eta/\kappa - \left[\eta/\kappa - W_0^{(1-m)}\right]e^{-(1-m)\kappa t}\right\}^{\frac{1}{1-m}} \qquad (6)$$

with W_0 = weight at time $t = 0$.

The case is somewhat different with respect to anabolism. The synthesis of high-molecular cell components needs, on the one hand, building blocks such as amino acids, sugars, phosphates, and so forth, and on the other hand energy which, in aerobic animals, is provided by oxidative processes. Both can be taken into account as limiting factors. The experimental results indicate that, so far as higher animals are concerned, there is a lawful connection between respiration, anabolism, and growth which works out in the following way.

The exponent m in our basic equation denotes the dependence of anabolism on body weight. If we insert for m that value which is experimentally found for the size dependence of resting metabolism, the growth laws for the organism in question follow automatically. Thus we can predict the growth type of an animal from its metabolic type, and this prediction has proved to be correct in a large number of cases, often in a quite unexpected way.

In a *first type*, respiration is proportional to the $\frac{2}{3}$ power of weight, according to the surface rule. Accordingly, the law of growth assumes the following form:

$$dW/dt = \eta W^{\frac{2}{3}} - \kappa W. \qquad (7)$$

We shall not bother with the mathematical elaboration, but show immediately the results. Fig. 3 gives metabolism and growth in the small aquarium fish, *Lebistes reticulatus*. Metabolic rates, measured as oxygen consumption, are presented in the log-log or allometric plot. As will be remembered, in the case of the surface rule the allometric regression line has a slope of $\frac{2}{3}$. So far as the growth curves are concerned, the solution of the growth equation gives theoretical

curves with the following main characteristics. First, growth rates are decreasing and growth eventually attains a steady state. Secondly, the curves for weight growth and linear growth are characteristically different. The curve of weight growth is sigmoid, with a point of inflexion at about one-third of the final weight. The curve of linear growth is a decaying exponential without a turning point. This is what we actually find experimentally.

This is the most common form of growth curves, found in fish, in a number of invertebrate classes and also, with certain restrictions, in mammals. The validity of these growth equations has been shown in many examples (Pütter, 1920; Bertalanffy, 1934, 1951a), and they have been adopted in applied biology.

It appears that the "Bertalanffy growth equation" is widely applied in international fisheries. It has been found to fit the commercially exploited fish species studied by the Fisheries Laboratory of the Ministry of Agriculture, Fisheries and Food at Lowestoft (England), with the possible exception of the hake (Wimpenny, pers. commun.). A comprehensive theoretical model of the dynamics of exploited fish populations has been developed, wherein growth of the species concerned is represented by equation 7 (Beverton, 1954; Beverton and Holt, 1957). Discussion of this population model (which, apart from fisheries, may well be adaptable to other populations) is beyond the scope of the present review. It should be mentioned, however, that examination of the various growth functions proposed led to the conclusion that "von Bertalanffy's growth equation is the most satisfactory of any that have hitherto been developed" (Beverton and Holt, *l.c.*). Ample data as well as description of mathematical analysis can be found in this work.

A relation similar to that stated by Bertalanffy et al. for the surface dependence of respiration was found by Yoshida (1956) in food intake. The quantity of plankton consumed by the sardine is proportional to the square of body length, and the same appears to be true for assimilating organs, such as the gill-rakers and the gut.

This characteristic course of growth is easily understood. If a body, with not too much change of shape, increases in size, its surfaces increase approximately with the second power of the length, but its volume and mass with the third power. Hence, the ratio between surface and

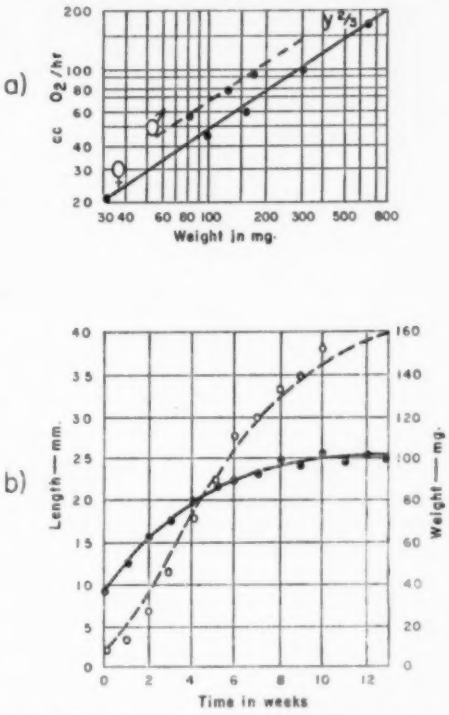

FIG. 3. THE FIRST METABOLIC AND GROWTH TYPE

Metabolic rate (a) and growth curves (b) in the Guppy (*Lebistes reticulatus*). Growth curves for ♀ ♂: ——— length growth; - - - - weight growth; calculated according to equation (7). After Bertalanffy and Müller (1943).

weight is continually shifted in disfavor of the surface. Consequently, so long as the animal is small, surface-proportional anabolism prevails over weight-proportional catabolism, and the animal grows. The larger it grows, the more the surplus remaining for growth decreases, and eventually a steady state will be reached where anabolism and catabolism balance each other, and growth comes to an end.

Now we come to the *second type*. We have said that in certain animals, for example, in insects, respiration does not follow the surface rule but rather is proportional to weight itself. Let us see what happens in this case (Fig. 4). The log-log plot of metabolic rate against body weight will give a line with a slope of 45°. On the other hand, we have to insert 1 for the exponent m in

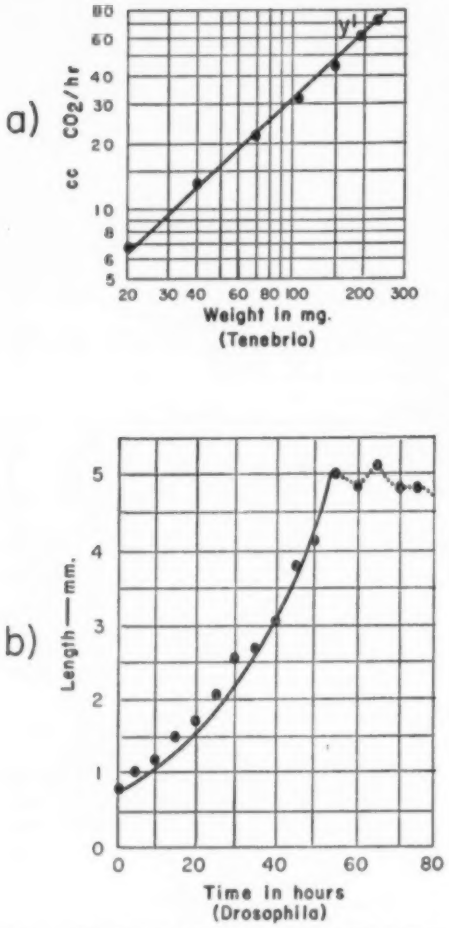

FIG. 4. THE SECOND METABOLIC AND GROWTH TYPE

Metabolic rate (a) and growth (b) curve (exponential) in insect larvae. After Bertalanffy and Müller (1943).

the growth equation, and thereupon get a completely different growth curve and a second growth type. In contrast to the first type, anabolism and catabolism, both being weight-proportional, run at the same pace. The more catabolism increases, the more does anabolism. Therefore, growth rates will not decrease but always increase, and the larger the animal becomes, the faster it grows. Growth is not limited but exponential, and no steady state is reached. This seems to be a paradoxical state of affairs, but is exactly what happens. Of course, an insect larva does not grow to any indefinite size. However, growth is stopped here by an altogether different mechanism. It is metamorphosis which abruptly intercepts the exponential increase, even causing a decrease in body weight as large amounts of tissue are broken down in order to develop the imago. The same metabolic and growth type also applies to hemimetabolous insects like the walking-stick, where there is no apparent metamorphosis, but the hormonal mechanisms responsible for development appear to be similar. Again, in land snails, which also belong to this type, exponential growth is intercepted by seasonal cycles.

Finally, we have described a *third metabolic type*, one where metabolic rate is intermediate between surface and weight proportionality, and which is exemplified by pond snails. Again we can calculate what growth curves are theoretically to be expected. If we insert a value $\frac{2}{3} < m < 1$ into the basic equation, it appears that the growth should follow a third type. The curve of weight growth does not differ very much from that in

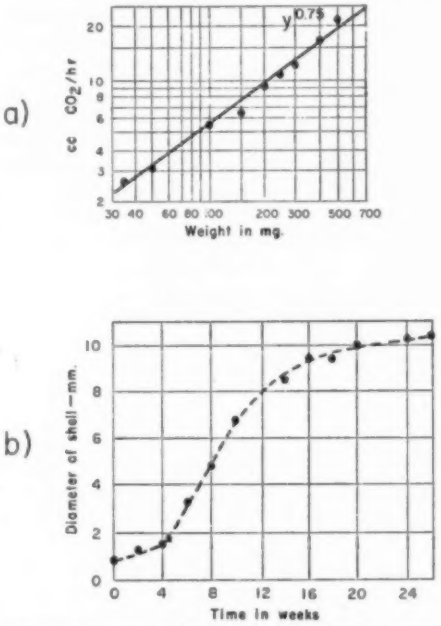

FIG. 5. THE THIRD METABOLIC AND GROWTH TYPE

Metabolic rate (a) and linear growth (b) (diameter of shell) in the ramshorn snail (*Planorbis* sp.). After Bertalanffy and Müller (1943).

TABLE 6

Metabolic types and growth types

Metabolic type	Growth type	Examples
I. Respiration surface-proportional	(a) Linear growth curve: attaining without inflexion a steady state. (b) Weight growth curve: sigmoid, attaining, with inflexion at ca. ⅓ of final weight, a steady state.	Lamellibranchs, fish, mammals
II. Respiration weight-proportional	Linear and weight growth curves exponential, no steady state attained, but growth intercepted by metamorphosis or seasonal cycles.	Insect larvae, Orthoptera, Helicidae
III. Respiration intermediate between surface- and weight-proportionality	(a) Linear growth curve: attaining with inflexion a steady state. (b) Weight growth curve: sigmoid, similar to I(b).	Planorbidae

the first type. Linear growth, however, is different, as its curve is S-shaped with an inflexion. Again, our prediction is verified (Fig. 5).

So in different animal classes there are different metabolic types and different types of growth, agreeing with theoretical expectation. Table 6 gives a survey of examples investigated, and may be considered as a first draft for a new chapter in physiology, namely, a *comparative physiology of growth*.

From the theory of growth just outlined, many consequences can be derived which have been verified empirically (cf. Bertalanffy 1957). Only one further example will be given. We can compare the values of the catabolic constant κ which were calculated from the growth curves, with the values of protein turnover as directly determined by experiment. In a number of cases, the constants have been verified with a degree of correspondence which is quite striking, since the theoretical model is admittedly oversimplified and, on the other hand, the error in the physiological determinations of protein turnover is considerable. For example, in 1938 the author calculated the turnover rate of protein from the growth curve of man. The value found was 1.165 g./kg. body weight/day. Eleven years later, Sprinson and Rittenberg (1949) calculated protein turnover from their experiments with N^{15}, and found a value of 1.3g./kg. body weight/day. Only a sound theory could have permitted such prediction.

GROWTH IN MAMMALS AND MAN

It is, however, obvious that the theory represents a first approximation, and that with further development revisions and the introduction of complicating factors will be necessary (for recent discussions of the theory, cf. Duspiva, 1955; Harms, 1955; Linzbach, 1955; Zeuthen, 1955; Bertalanffy, 1957).

A case in point is growth in mammals. From the viewpoint of metabolism, it may be said that, in a first and crude approximation, mammals appear to belong to our first type, where the surface rule of metabolism applies. Indeed, the surface rule was first stated by Rubner for mammals, and it was already mentioned that the clinically important case, the determination of basal metabolism in man, applies the surface rule in the somewhat modified form of the Dubois standard formula. Correspondingly, mammalian growth roughly follows the characteristic pattern of the first growth type discussed.

In detail, however, there are complications. Unfortunately and somewhat paradoxically, there are relatively few good data suitable for this type of analysis.

If the basal or resting metabolism in the rat (Fig. 6) is measured over the entire life span, it appears that as a crude overall approximation the surface rule obtains, that is, the overall allometric regression line has a slope of about $\frac{2}{3}$. In more detail, however, there is a break in this line, such that the first part of the allometric line is steeper, and the second part much flatter, than would correspond to a slope of $\frac{2}{3}$. The break takes place at a body weight of about 100 g., that is, preceding sexual maturation. As we have found in other investigations (Bertalanffy and Pirozynski, 1952, 1953), similar breaks appear in quite a

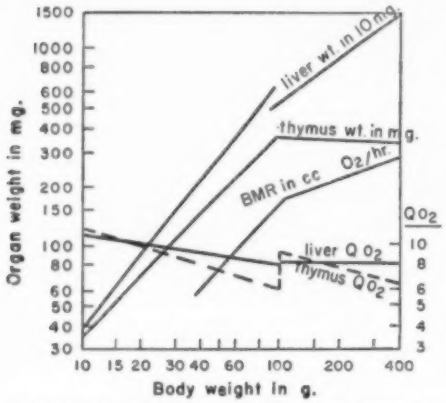

FIG. 6. DISCONTINUITIES OF RELATIVE GROWTH IN THE ALBINO RAT

All discontinuities appear at a body weight of approximately 100 g., i.e., before puberty. A corresponding discontinuity is found in the growth of the entire animal (see Fig. 7). Only regression lines are shown in the figure; individual data and statistical analysis are given in the original papers. After Bertalanffy and Piozynski (1952, 1953) and Racine (1953).

number of physiological characteristics, at the same age and body size: in the allometric growth of the liver, the involution of the thymus, the tissue respiration of liver and thymus, and certainly there are others (Fig. 6). There is small wonder that these breaks and shifts are found, as the coming into play of the sex hormones entails a deep-reaching change in the entire metabolic pattern.

On the other hand, the growth curve of the rat was analyzed long before the physiological studies just mentioned (Bertalanffy, 1938, 1951a; a discussion of recent literature on rat growth is given in Bertalanffy, 1957). The result was found that the growth of the rat follows the first growth type, with a characteristic change, however, in the values of the constants, again at the critical point of around 100 g. body weight. If these growth cycles are taken into account, an excellent fit of the empirical growth curves by means of our formulas can be obtained (Fig. 7).

So it would appear that mammals belong to the first type, with the qualification, however, that two growth cycles must be distinguished, the transition from the first to the second cycle taking place at the time of sexual maturation. This is to be considered no more than a first approximation.

However, there is one organism whose growth curve is different from all others. Since our growth formulas apply to a large number of species, the shapes of their growth curves are the same, and the same curve can be used to represent the growth of various species, simply by taking different scales for time and body size. Fig. 8 shows the growth curves of a fish and a mouse. The latter, similar to that of the rat, also shows a growth cycle in detailed analysis, which does not much alter the picture. If, however, the growth curve of man is entered, it appears to be unique.

The second part of the curve, beginning with puberty, follows the general pattern. The first part, however, is very different. In infancy and childhood, the curve is enormously protracted. A new growth cycle is added, as it were, to the typical pattern of growth. Although this change is heralded in the growth cycles of lower mammals, only in man does it lead to a singular shape of the growth curve. This growth curve of man, abnormal as it were, is of course connected with changes in the hormonal balance. This is demonstrated by pathological cases, such as *pubertas praecox* in pituitary dysfunction, when puberty takes place at an early age, as it does in other mammals and still in apes. The singular growth curve of man is a quantitative expression of the retardation of human development which, according to Bolk (1926), is one of the basic factors in the evolution of man. At the same time, it is an important factor for his uniqueness in nature. Animals run through their developmental period speedily, and

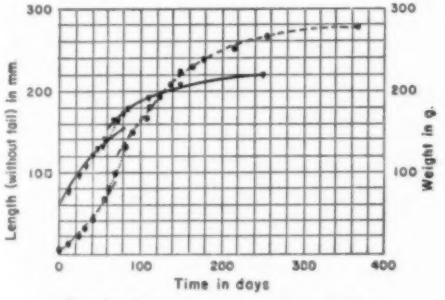

FIG. 7. GROWTH OF THE ALBINO RAT

Donaldson's data (♂). Length growth ———, weight growth – – – –, calculated according to equation (7). The calculation shows two growth cycles, with a break at approximately 100 g. body weight. Donaldson's data are today not considered to be optimal, since modern laboratory diets have increased the growth in the rat. The figure shows, however, the excellent numerical fit that can be obtained with the theoretical formulas. After Bertalanffy (1941b).

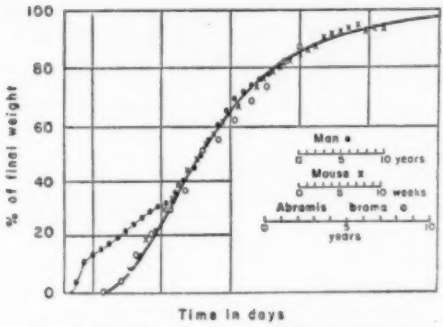

FIG. 8. COMPARISON OF THE GROWTH CURVES OF A FISH, MOUSE, AND MAN

After Bertalanffy (1951a).

soon they reach puberty and the adult stage. Man, on the other hand, is given a long period of youth, and is thus enabled to learn and to collect experience. Thus the characteristic human growth curve is a prerequisite for that mental development and civilization which so sharply distinguishes man from all other beings.

ACKNOWLEDGMENT

This essay is based upon work carried through in the author's laboratories at the University of Vienna and the University of Ottawa (Canada). Part of this work was aided by research grants from the National Research Council, the National Cancer Institute, and the Humanities Research Council of Canada. A survey of the problem of animal growth in general is given in Bertalanffy, 1951a, and 1957.

SUMMARY

Work aimed at establishing connections between metabolism and growth is reviewed. In the various animal classes, three "metabolic types," i.e., forms of dependence of metabolic rate on body size can be distinguished: proportionality of metabolic rate to surface area, or to weight, or one intermediate between surface and weight proportionality. The various theories regarding the size dependence of metabolism are discussed, with particular consideration of the relation of tissue respiration to body size. Corresponding to the "metabolic types" mentioned, there are "growth types" distinguished by different growth curves of the species concerned. A general theory of animal growth, advanced by the author, permits explanation of the connection between metabolic types and growth types. The theory is illustrated by examples taken from invertebrate and vertebrate classes. Mammalian and human growth, while generally following the "first growth type," show breaks in the growth curve connected with puberty. The data and concepts presented herald a new chapter of physiology, the comparative physiology of growth.

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A THEORY OF THE CONTROL OF DIFFERENTIATION IN THE CELLULAR SLIME MOLDS

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IN THE life history of cellular slime molds separate independent amoebae aggregate in masses, and each of these masses proceeds to develop as a unified individual. Some of the amoebae within the mass differentiate into stalk cells, and the remainder differentiate into spores. Depending upon how many amoebae enter the aggregate, there is a wide variation in the size of the fruiting bodies. Yet there is a constant relationship between the number of stalk cells and the number of spore cells. This problem of proportional development is of basic importance not only in the slime molds but in all organisms exhibiting regulative development.

My colleagues and I have ascertained many pertinent facts on this proportionality of development in the slime molds in earlier work, and some new original information will also be included here. From this whole array it is possible to construct a theory which ties these facts together. There is no assurance that the theory represents the actual mechanism of development, and certainly alternative theories could be proposed that would fit the facts. This particular theory, however, has the merit of simplicity, and does serve to illustrate what kind of a mechanism could conceivably be operating in the development of these organisms.

Before describing the theory it will be well to review some of the known facts, and to present some original material that will serve as a basis for the theory. But since there may be some readers who are not completely familiar with the cellular slime molds, I shall first discuss briefly the life history of *Dictyostelium discoideum* and then compare it with some related species.

The spores of *D. discoideum* are covered with a hardwalled capsule. Upon germination each capsule liberates one amoeba. The amoebae divide mitotically and remain entirely separate from one another, feeding independently upon bacteria. When they multiply to a population of sufficient numbers, they stream together to form large collections of many cells or pseudoplasmodia, and this aggregation process appears to be largely due to a chemical substance, acrasin, to which the amoebae are chemotactically sensitive. Certain of the amoebae, which form the center of the aggregate, apparently produce it sooner than others, and in this way an acrasin gradient is set up which is effective in orienting the amoebae.

The aggregated cell mass assumes a sausage shape and crawls about the substratum for variable periods of time. During this migration phase it is sensitive to light and heat gradients, orienting itself toward light and toward warmer regions. Differentiation begins at this stage. The anterior cells of the sausage are destined to become part of the supporting stalk and the posterior cells will turn into spores. The final fruiting involves a series of morphogenetic movements in which the anterior presumptive stalk cells are pushed down through the spore mass, and in so doing, these stalk cells become large and vacuolate and are permanently trapped in a delicately tapering cellulose cylinder. During this culmination stage, the spore mass is lifted up into the air and each amoeba in the mass becomes encapsulated into a spore (Fig. 1).

In *Dictyostelium mucoroides* and *D. purpureum* there is a basically similar development, except for the fact that during the migration period the stalk is formed continuously. Its formation begins right after aggregation, and as the cell mass crawls across the substratum, again strongly oriented towards the light and heat, the stalk is constantly deposited at the tip (Fig. 1). The only exception to this, as Raper and Thom (1941) have found, is that in certain strains there are periodic discontinuities in the stalk, which indicate occasional intervals of migration without stalk formation.

The genus *Polysphondylium* represents another type of development which bears many similarities

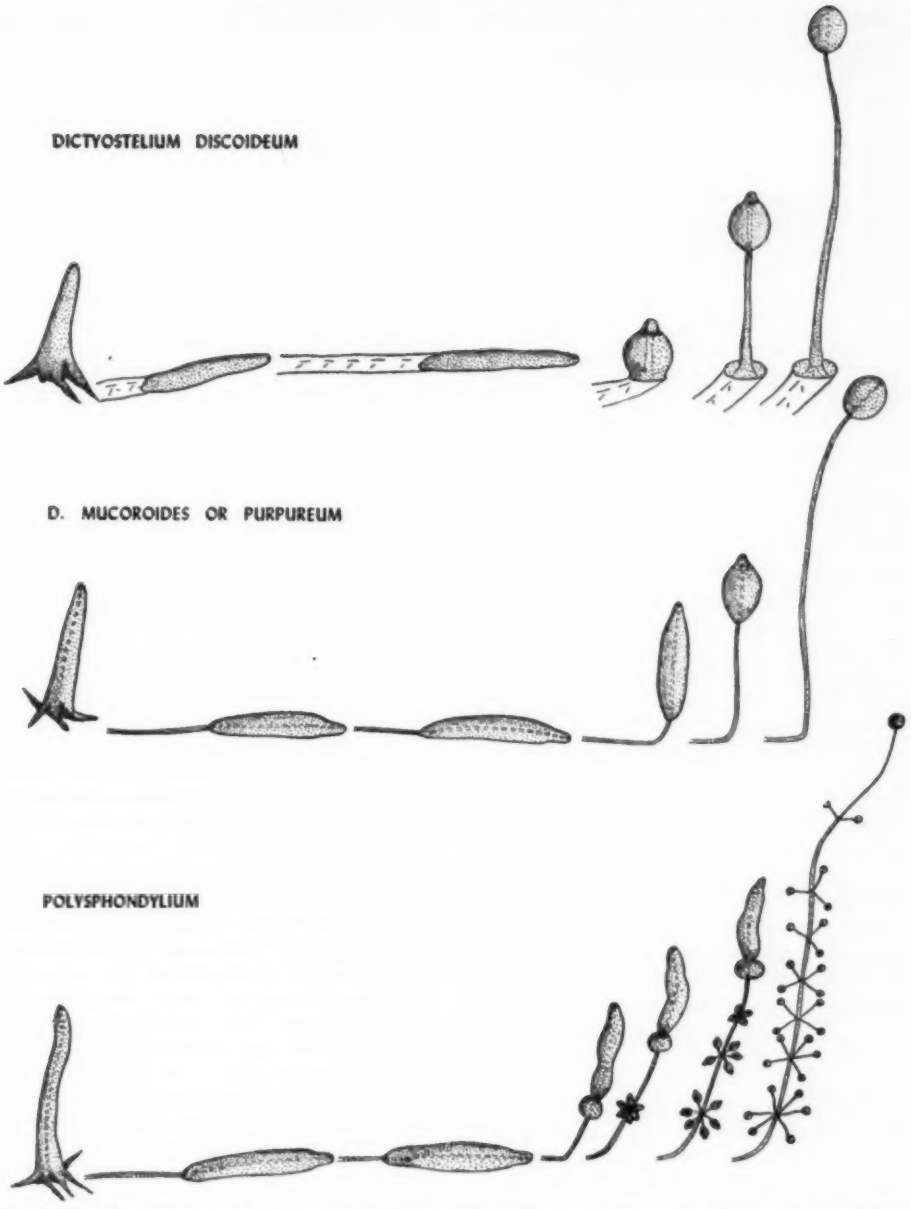

FIG. 1. THE MIGRATION AND CULMINATION STAGES IN THREE DIFFERENT TYPES OF CELLULAR SLIME MOLDS

to the *D. mucoroides* type, but differs in the pattern of the final fruiting. After a period of migration, while again the stalk is being continuously constructed, the cell mass breaks into fragments in the posterior portion, leaving behind a series of cellular collars about the stalk that cease all forward movement. Each of these doughnut-shaped cell masses breaks up into several

radially oriented secondary fruiting bodies, so as to give the appearance of a series of whorls arising at fairly regular intervals, with one large *D. mucoroides*-like sorus at the tip (Fig. 1).

The theory to be proposed shortly is designed to explain certain aspects of this remarkable kind of development found in the cellular slime molds. The best way to expose the problem to be illuminated is to frame three questions, and in attempting to answer each of these questions some understanding of a possible mechanism of the control of differentiation can be obtained. The three questions will be stated briefly first, and then each one will be examined in detail.

(1) One of the basic facts is that there is a differentiation in which two cell types are produced, the stalk cells and the spore cells. As previously mentioned, the stalk cells are produced at the anterior end of the cell mass, and the spore cells at the posterior end. So the first question to ask is: *what are the differences between the front and the hind ends of the mass?*

(2) There occurs normally in these molds a great variation in size of the cell mass. Since feeding ceases before aggregation, the total size of the aggregate depends upon the quantity of amoebae that enter into it, and large fruiting bodies may in extreme cases be a thousandfold larger in volume than small ones. Nevertheless, the size of the spore mass bears a constant, proportional relationship to the size of the stalk, and our second question is: *how, in any one species, is it possible that the differentiation remains proportionate irrespective of size?*

(3) In recent studies we have shown that different species (and even different strains of one species) have different proportionality relationships. Therefore the third question is: *how can one account for differences in proportionality ratios in different species and strains?*

THE DIFFERENCES BETWEEN THE FRONT AND HIND ENDS OF THE MASS

The facts relevant here have mostly been presented previously, and it is necessary only to summarize and bring out some of the pertinent points. For simplicity, the situation in *D. discoideum* will be used as the main example, and the variations of the other species will be added later.

In the first place, it was found that if all the amoebae were stained with a vital dye such as Nile blue sulfate, Bismarck brown, or neutral red before aggregation, then after aggregation the migrating cell mass would appear uniformly stained. At a later period, however, the anterior, presumptive stalk end remained dark, while the posterior, presumptive spore portion blanched (Bonner, 1952). The division line between these two zones remained sharp and distinct as the migrating mass crawled over the surface of the substratum. The limitation of these experiments is that while they provided an excellent tool for revealing vitally the extent of the early presumptive stalk and spore areas, they give little indication as to what might be the chemical and physical basis of such changes.

Another approach was to measure cell and nuclear sizes (Bonner and Frascella, 1953; Bonner, Chiquoine, and Kolderie, 1955). Both measurements were consistent in that they showed that during a period where a division line was evident after using vital dyes, the anterior cells and their nuclei were larger than those of the posterior portion. In the studies on nuclear size it was shown that this difference was only evident after a period of migration, for very young migrating cell masses showed no differences between the nuclei of the front and hind ends.

The most illuminating studies of the difference between these two regions were those performed using histochemical techniques in collaboration with Dr. Duncan Chiquoine of Princeton University. In particular, the examination of the distribution of non-starch polysaccharides showed that at the onset of migration the cell mass was evenly stained, but that after a period of crawling the posterior cells contained small, dense, intensely stained granules of non-starch polysaccharides, while the anterior cells were, by comparison, pale and diffuse in their staining reaction (Fig. 2). However, it was clear from sections of the culmination stage that the anterior presumptive stalk cells did contain non-starch polysaccharides which accumulated in their centripetal ends as they advanced into the tip of the cell mass. Their orientation is radial, and obviously they are secreting the cellulose cylinder. When largely depleted, they arrive at the tip and become incorporated into the stalk, the cellulose cylinder that they themselves have manufactured (Bonner, Chiquoine, and Kolderie, 1955). Once in the stalk they progressively swell and become large and vacuolate.

In the same histochemical study we examined

the distribution of alkaline phosphatase. In late migration the anterior presumptive stalk cells were clearly high in alkaline phosphatase, and in the culmination stage this difference was even more sharply defined. However, little or no activity was shown by the cells once they had entered the stalk.

So in answer to our question of what are the differences between the front and hind ends, we can say first off that there are numerous demonstrable differences, and undoubtedly many which have yet to be revealed. But the mere listing of differences is in itself of limited interest; it is desirable to attempt to attribute some meaning to these differences.

Consider a fruiting body in its mature form. It is obvious that since it sticks up into the air it is dependent upon the rigid cellulose cylinder of the stalk. The basis of its form, its skeletal support, comes from the production (and proper distribution) of polysaccharide. The anterior cells, then, are the active cells as far as the morphogenesis of this organism is concerned; they are the ones responsible for the final form. It is impossible at our present state of knowledge to ascribe any specific task to the presence of high alkaline phosphatase, but again it is consistent with the notion presented here that the front end is active and vital in development. This idea is also supported by the work of Gregg, Hackney, and Krivanek, (1954) who found that there is an appreciable loss of protein nitrogen during culmination (presumably used as an energy source for carbohydrate synthesis), and that this loss occurs only in the stalk region.

The activity of the anterior pre-stalk cells is indeed striking, and yet in the final fruiting body the mature stalk cells are mostly trapped and dead inside the stalk cylinder. From these twin facts it is hard to avoid the conclusion that the stalk cells have thrown themselves into their morphogenetic activities with such energy that they have lost the ability to perpetuate themselves, and that instead they become depleted, exhausted, inert bricks that fill up the inside of the stalk.

The presumptive spores, on the other hand, appear to give off nothing; they neither show a high enzymatic activity (viz., of alkaline phosphatase), nor are they wasteful of their polysaccharides. They would seem to be conserving all for the next generation and they make little or no contribution to our immediate understanding of

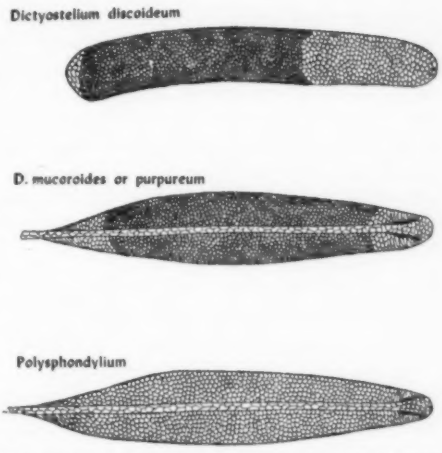

FIG. 2. THE STAINING PROPERTIES OF THE CELLS DURING THE MIGRATION PHASE FOR THREE DIFFERENT TYPES OF CELLULAR SLIME MOLDS

morphogenesis. When one considers the activity of these two cell types, it is indeed a striking division of labor.

In turning to comparative studies of other species, the *D. mucoroides* type (which includes *D. purpureum*) shows much the same pattern except for the fact that the presumptive stalk region appears consistently smaller. The significance of this point will be discussed later (Fig. 2). *Polysphondylium*, on the other hand, shows none of these early signs of differentiation; both the front and hind cells appear, even after considerable migration, to be evenly stained by the methods previously mentioned. Differentiation occurs very suddenly at the end of its cycle, after the doughnut-shaped rings of cells have been cut off and left behind. As pointed out previously (Bonner, Chiquoine, and Kolderie, 1955), this prolongation of youthful, embryonic characters until the last moment may be correlated with the ability of *Polysphondylium* to fragment into small fruiting bodies after a period of migration. But even in this case the sequence of events in differentiation must be basically the same, the only unusual aspect being its timing mechanism.

In conclusion, it should be emphasized that the principal difference between the front and hind ends is one of activity. There are reactions taking place in the front end which are crucial to the morphogenesis of the organism and which have no counterpart in the hind end. There are, of

course, still many questions one would like to ask about these reactions. It would be desirable to have a fuller understanding of the chemical changes involved; for instance, to learn if there is any relation between this anterior activity and the fact that the front end is always the region of high acrasin emission (Bonner, 1949). But now that we have underlined some of the major antero-posterior differences we can attack the problem of proportionality.

HOW, IN ANY ONE SPECIES, IS IT POSSIBLE THAT DIFFERENTIATION REMAINS PROPORTIONATE IRRESPECTIVE OF SIZE?

The first thing that must be done is to give the evidence that proportionality does hold in the slime molds. A superficial examination of a culture of *D. discoideum* under the dissecting microscope makes one strongly suspect that such is the case, for both the small and large fruiting bodies will have a similar appearance. This was pointed out by Raper (1935) in his original description of the species. If one takes the pains to measure these mature fruiting bodies accurately, as we did some years ago (Bonner and Slifkin, 1949), then it is clear that with increase in size the sorus volume is roughly linearly proportional to the volume of the mature stalk.

Recently (in collaboration with Miss Marcia J. Shaw) we have studied the proportions of the anterior presumptive stalk cells and the posterior presumptive spore cells in the migrating stage. Of necessity we had to use different techniques for the different species. The most desirable method, which would work only with *D. mucoroides* and *D. purpureum*, was to make fixed and stained whole mounts of the cell masses, using a methylene blue technique developed by Mr. Vincent R. Gregg, Sr., of this laboratory (See Appendix). From camera lucida drawings of the migrating masses, their volumes were calculated by approximating each part to the form of a cylinder. With *D. discoideum* the method of measurement was the same, but the camera lucida drawings were made of live cell masses stained vitally with Nile blue sulfate (Bonner, 1952).

As one can see from Fig. 3, there is a straight line relationship if, for *D. discoideum* and *D. mucoroides*, the volume of the presumptive stalk region is plotted logarithmically against the volume of the presumptive spore mass or sorus. To avoid anticipating the next question, I will not compare the two species at the moment, but rather would like to point out that in each case there is proportionality, and that in *D. mucoroides* especially it extends over a considerable size range. This means, then, that not only is the final differentiated product proportional, but so are the presumptive areas as well.

One of the most interesting aspects of proportionality is to be seen in the phenomenon of regulation. This was beautifully illustrated in a pioneer experiment of Raper (1940) in which he cut migrating pseudoplasmodia of *D. discoideum* into fractions and noticed that each fraction gave a normal fruiting body, although, this took some additional time to be achieved in the anterior portion. (Fig. 4).

This experiment has been repeated a number of times, both using the vital dye method (Bonner, 1952) and using the method which stains specifically for the non-starch polysaccharides (Bonner, Chiquoine, and Kolderie, 1955). From these studies it is possible to show that the staining properties so characteristic of the anterior and posterior regions are actually reversible. In Fig. 5 one can see that one hour after the all-dark posterior portion of presumptive spore cells has been isolated, there begins to appear a small pre-stalk area at its tip, and by six hours a small but normally proportional cell mass is evident. The converse is true of the isolated tip, inasmuch as it shows a progressive appearance of presumptive spore cells at its posterior end. Clearly, in both cases there has been a reversal of the fate of the cells (which follows Driesch's dictum in that they are determined by their position in the whole) as well as of their staining properties.

Fig. 3, which shows the proportionality of the presumptive spore and stalk areas in the two species of *Dictyostelium*, reveals an interesting point which concerns regulation. Methods have been devised to encourage extensive, long migration in both *D. discoideum* (Slifkin and Bonner, 1952) and *D. mucoroides* (Bonner and Shaw, in press). In both these species, when the methods previously mentioned are used, it is possible to check the proportions at different points during an extended migration up to 70 mm. in length. In neither species did the proportions show any alteration after prolonged migration. In all cases the points remained on the lines indicated in Fig. 3. This is especially significant in the case of *D. mucoroides*, for in that species, as migration

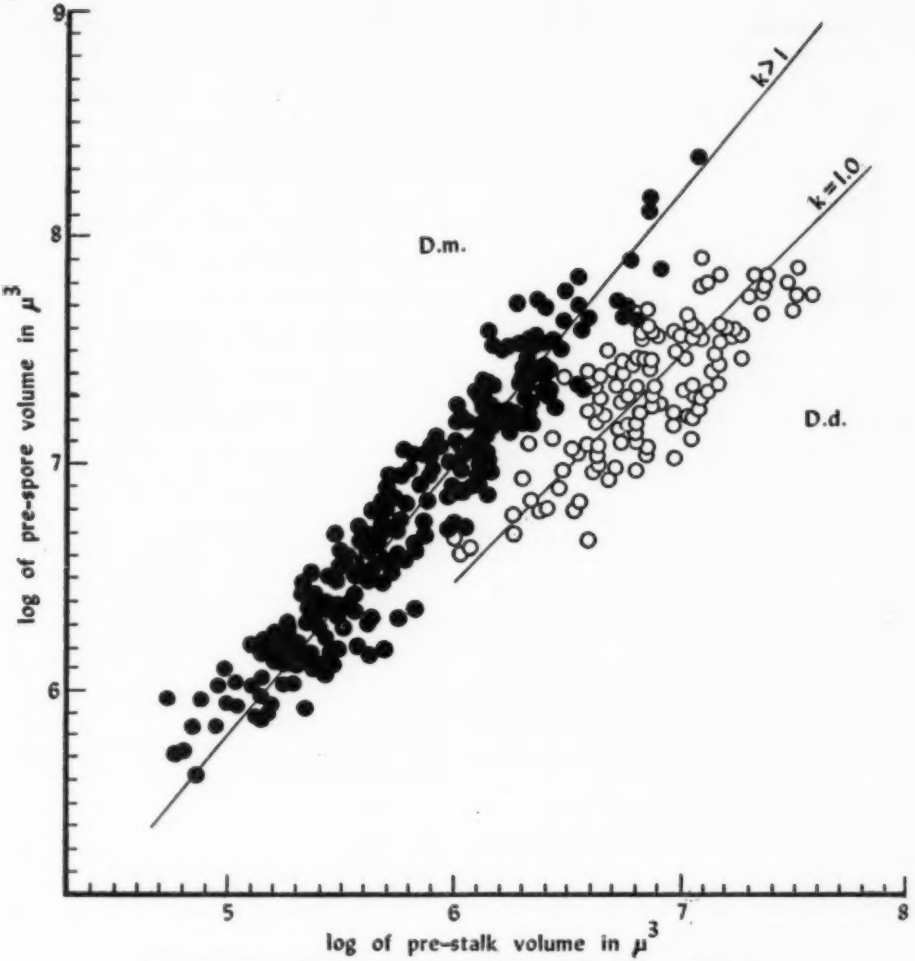

FIG. 3. PRE-SPORE VOLUME PLOTTED LOGARITHMICALLY AGAINST PRE-STALK VOLUME FOR *D. MUCOROIDES* AND *D. DISCOIDEUM*

The slopes of the lines (k) are roughly indicated. The solid dots actually include 6 strains of *D. mucoroides* tested, all of which were similar, as were 3 strains of *D. purpureum* which are not included. The only exception is DM-4, which gave points parallel to, but above the other *D. mucoroides* strains. See text for details.

continues, there is a constant loss of cells into the stalk, since this structure is being formed at all times. In other words, there is a continuous disappearance of cells at the tip, but since the division line shows a fixed proportionality, it must be constantly regulating, by moving posteriorly. If a cell mass is large in the beginning, its proportions will be such that it will lie on the upper end of the curve for *D. mucoroides* in Fig. 3. With extended migration (up to 220 mm. in some cases), the mass will become smaller and move down the curve so that when it finally fruits it will have a gigantic stalk 220 mm. long and a minute sorus, although at any point in its journey the presumptive areas will show proportionality.

At this point a hypothesis may be proposed which is perhaps the mosts important element in the whole theory. To account for proportionality

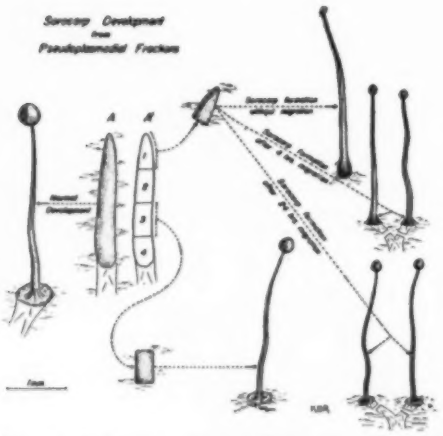

FIG. 4. COMPARISON OF THE FRUITING OF ENTIRE CELL MASSES WITH DIFFERENT FRACTIONS OF THE SAME

If apical fractions fruit immediately they show abnormal proportions, but with some migration the normal proportions are resumed (from Raper, 1940).

and regulation it must be assumed that one part of the cell mass "knows" the extent of another. When a pre-stalk tip is isolated, the information that all the posterior pre-spore cells are missing is somehow registered, so that in a matter of a few hours the deficit is made up and regulation has taken place. A logical conclusion is that there must be some communication between parts. Let us therefore postulate a polar movement of some key factor which provides the necessary information. In our previous example, if the posterior portion is removed, so also is a large source of the polar factor, and consequently regulation ensues. If the anterior portion is removed, then although there may still be an appreciable supply of polar factor in the posterior portion, the anterior reaction which is dependent upon the polar factor must start and establish itself at the new tip. An equilibrium, i.e., a balance between the movement and the reaction, will soon result. The nature of this balance will be discussed shortly, but at the moment two things in this hypothesis need further clarification: the nature of the factor, and the way in which it is transported in a polar fashion.

A number of observations make it very tempting to suggest that the polar factor can be transported by especially fast-moving cells, which in essence serve as polar messengers. It is an old observation that the cells do not keep a rigid relation one to another during migration, but that their speeds are variable and independent (Bonner, 1952). Now a series of experiments was done in which a posterior half of a migrating cell mass of *D. discoideum* stained vitally with Nile blue sulfate or neutral red was grafted onto a colorless anterior half, and the extent of the dye was then followed for a number of hours. It could be seen with the dissecting microscope that a number of intensely stained cells would form a front echelon and stream towards the anterior tip, so that within approximately six hours these fast cells would cover half the length of the actively migrating mass (Fig. 6). That this is the result of some cells being especially rapid in movement and not simply a consequence of diffusion is supported by a previous experiment, one in which an anterior, vitally stained group of cells was grafted into an intact, colorless migrating mass. In a matter of approximately three hours these cells moved to the tip, but in this case the final result was not an all-colored cell mass, as in the first case, but instead the colored cells moved up as a band (Bonner, 1952). From this we may conclude that the anterior cells are fast-moving and the posterior ones are slow.

If a colorless posterior portion is grafted onto a vitally dyed anterior portion the color will move backward at approximately the same rate as the forward movement just described. Therefore, as one would expect in a variable population of cells, there are not only especially fast cells but especially slow cells as well. We have some further interesting information about the slow cells: in *D. mucoroides* they apparently accumulate in the posterior end of the migrating mass so that if migration occurs over an extended period, then there is a steady increase in the accumulation of slow cells (Fig. 7). It is possible to discern these cells both in the total mounts when using Gregg's methylene blue technique and also in the technique for the non-starch polysaccharides (see Fig. 2). In fact, it is evident from the latter procedure that these accumulating slow cells resemble the anterior presumptive stalk cells, for they are large in size and show the typical anterior staining properties (Bonner, Chiquoine, and Kolderie, 1955). It is possible that these cells have participated in the anterior, energy-consuming reaction, but have escaped becoming incorporated into the stalk, and that now, since they are low in every resource, they

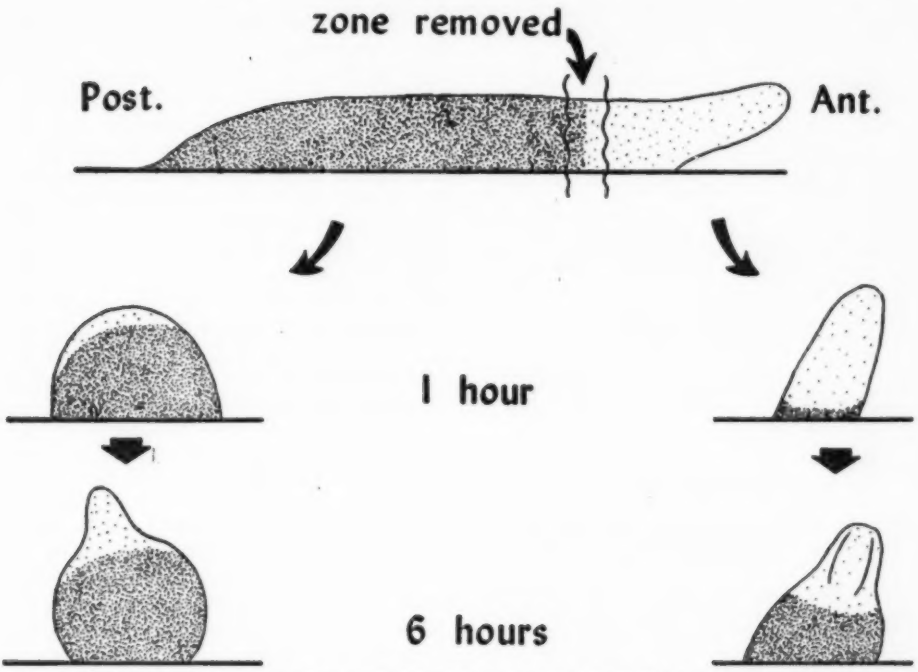

FIG. 5. A DIAGRAM ILLUSTRATING THE EXPERIMENT IN WHICH A PARTIALLY DIFFERENTIATED MIGRATING CELL MASS IS BISECTED AND EACH PORTION IS EXAMINED BY THE PERIODIC ACID—SCHIFF METHOD AFTER 1 AND 6 HOURS RESPECTIVELY

Note that the anterior end of each fragment reversed its staining properties; in one case from the light pre-stalk condition to the dark pre-spore condition, and vice versa in the other (from Bonner, Chiquoine, and Kolderie, 1955).

drop back to become laggards. However, these slow cells do maintain the ability to regulate, and therefore they cannot be too low in energy. It was possible in a number of cases of *D. mucoroides* showing prolonged migration to cut off these cells, and in every instance they gave rise to normal fruiting bodies.

The fact that there is such a group of cells following the pre-spore mass during culmination in *D. discoideum* is a familiar observation (Bonner, 1944; Raper and Fennell, 1952). Furthermore, in the sectioned material of migrating pseudoplasmodia we have made recently, it is possible to observe a small zone of cells having pre-stalk characteristics, and closely resembling the situation observed in *D. mucoroides*. It is interesting that this group of laggard cells would account for the basal disc, a distinguishing feature of *D. discoideum* and the one from which it derives its name. The idea is that this group, which has pre-stalk characters and which is located posteriorly, will naturally surround the base of the stalk as culmination proceeds; furthermore, its cells will ultimately become large and vacuolate, following the same course of cellular differentiation as the stalk cells proper.

However, if this were so, one might expect that with prolonged migration the basal disc would become excessively large, which is not the case. Its size is clearly independent of the duration of migration. The answer to this paradox is found in the well-known fact that during migration there is a constant loss of cells deposited singly and in small groups in the collapsed slime sheath left behind. This loss will largely account for the fact that upon prolonged migration the cell masses become continuously smaller (Bonner, Koontz, and Paton, 1953). We have recently measured this cell loss by counting the cells along a slime track and found that there is considerable varia-

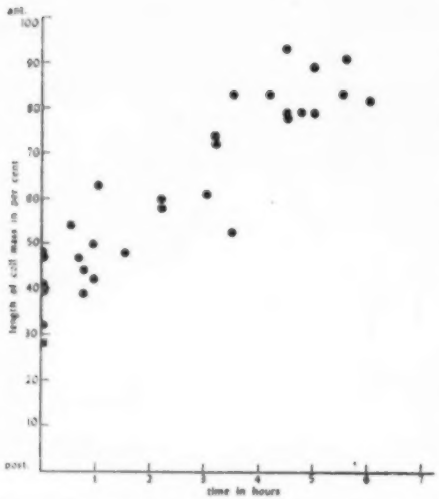

FIG. 6. THE SPEED OF FORWARD MOVEMENT OF CELLS STAINED WITH VITAL DYES IN MIGRATING PSEUDOPLASMODIA OF *D. DISCOIDEUM*

The ordinate shows the position of the marked cells after a colored posterior portion has been grafted onto a colorless anterior portion. The abscissa is time, and it is clear that after six hours the fastest colored cells have reached the tip region.

tion among individual pseudoplasmodia. The rate of cell loss may be high or low at first, but after a migration of 25 mm. the rates rise or fall to a fairly uniform, low rate of approximately 5 to 10 cells per mm. of migration, and then it rises steadily so that by 60 mm. of migration the rate of loss may be anwhere from 10 to 30 cells per mm.

To return to the matter of the fast cells which are possibly bringing the polar factor to the anterior zone, two further points should be added. One is simply that there is no need to postulate any special substance or substances for the polar factor. It could be a simple matter of food or some substrate necessary for a particular enzyme reaction. The characteristic of the front end is activity, and for this energy is necessary. The speed of the cells would imply an energy-rich condition, all of which would fit together. It is of course also conceivable that the cells move anteriorly in an acrasin gradient and that the substrate may contribute to the continued high production of acrasin at the anterior end, but unfortunately the connection with acrasin is especially speculative.

The other point to be made concerning the polar factor is that there is some evidence to support the contention that the amount of the factor produced depends on the total number of cells or the total volume. If short and fat migrating masses of *D. mucoroides* are compared with extremely thin and long ones, they will appear to have different proportions if the linear distance of the pre-spore and pre-stalk zones are used, but if they are calculated on the basis of volumes they represent a harmonious group (Fig. 8). In other words, the notion that a certain percentage of the total population of cells are fast cells is supported.

To summarize the reply to this second question, an attempt has been made to provide a rational hypothesis which accounts for proportionality and the related phenomenon of regulation. It is suggested that there is a polar movement of substances which provides a communication between parts by delivering these essential substances to the anterior end, where there are reactions responsible for the morphogenesis of the slime mold. Furthermore, it is suggested that this polar movement is achieved by especially fast-moving cells, although it must be remembered that proportional development is also possible in minute fruiting bodies possessing as few as 12 cells (Sussman and Sussman, 1956). In such small pseudoplasmodia there is perhaps no transport, but rather a simple depletion of the factor that is already present in the two anterior cells that make up the stalk.

HOW CAN ONE ACCOUNT FOR DIFFERENCES IN PROPORTIONALITY RATIOS IN DIFFERENT SPECIES AND STRAINS?

In Fig. 3 the volume of the pre-stalk area is plotted logarithmically against the volume of the pre-spore area, and each of the two species has a curve that approximates a straight line. The slope and the position of the two differ, however. Furthermore, there is a particular strain of *D. mucoroides* (DM-4) whose points are parallel to, but not coincident with, other strains of *D. mucoroides*, which means that there are three known proportionality relationships.

A straight line on such a logarithmic plot indicates a so-called allometric relation (Huxley, 1932) and can be written in the form

$$y = bx^k$$

or,

$$\log y = \log b + k \log x$$

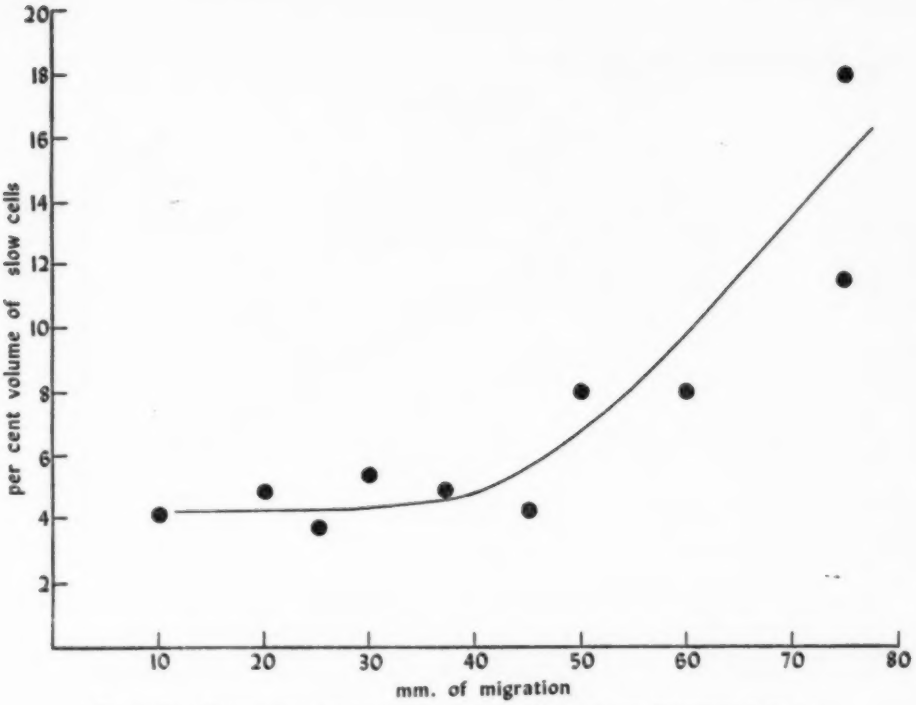

FIG. 7. THE PROGRESSIVE ACCUMULATION OF SLOW CELLS IN THE POSTERIOR END OF *D. MUCOROIDES* AFTER PROLONGED MIGRATION

Each point represents a mean of about 10 pseudoplasmodia.

In this case y and x are the pre-spore and pre-stalk volumes respectively, k is the slope of the line, and b is a constant. In glancing at Fig. 3, it may be seen that in *D. discoideum* the slope is approximately 1, while in *D. mucoroides* the slope is greater than 1. In the strain DM-4 the slope appears to be similar to other strains of *D. mucoroides*, but differs in the constant b.

With the generous help of Dr. Martin Wilk of the Mathematics Department of Princeton University, it has been possible to check these assertions statistically. It was found desirable, in this analysis, to plot the logarithm of the pre-spore volume against the sum of the log of the pre-spore and the log of the pre-stalk volumes, for in this way the variability is confined mainly to one variable, namely, the pre-spore volume (Fig. 9). On such a plot the slope of the *D. discoideum* curve should now be 0.5, and the slopes of the *D. mucoroides* curves should be >0.5. Using a least square analysis, the slope of *D. discoideum* is 0.4865 ± 0.0488, *D. mucoroides* 0.5361 ± 0.0126 and DM-4 0.5295 ± 0.0180, where the allowance is twice the standard error of the estimate.

By means of significance tests (see Appendix) it is possible to say that we may reasonably assume that the slope of *D. discoideum* is 1 (when plotted allometrically as in Fig. 3), and also that each of the two *D. mucoroides* strains has the same slope and that this slope is greater than 1.

Now comes the problem of extending the basic hypothesis concerning proportions so that these new facts may be included. Let us assume that the polar factor (S) can be used in two related reactions, one involving stalk formation and the other involving the formation of the characteristic pre-stalk condition that results in the formation of a division line (Fig. 10). There are here three processes whose rates will be important in the over-all mechanism: the rate of polar movement and therefore the supply of S (k_1), the rate of utilization of S in stalk formation (k_2) and the

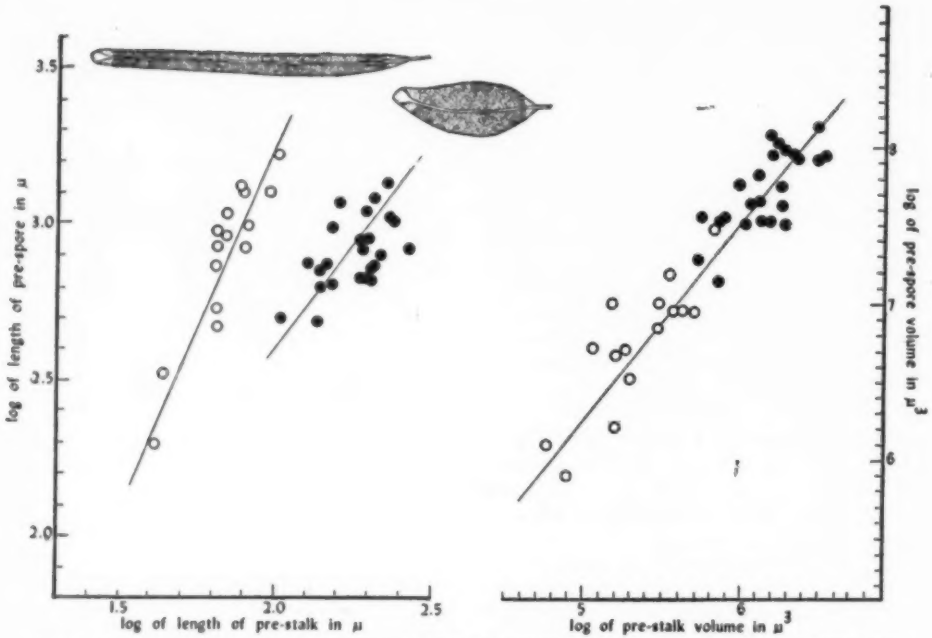

FIG. 8. A COMPARISON OF THE LOGARITHMIC PLOTS OF LINEAR MEASUREMENTS OF THE PRE-SPORE AND PRE-STALK ZONES (LEFT) WITH THE VOLUMES OF THE SAME ZONES (RIGHT), FOR BOTH THIN AND FAT CELL MASSES OF *D. MUCOROIDES*

Note that when the volumes are used the data fall into one continuous curve.

rate of utilization of S in pre-stalk formation (k_3). We must also make the assumption that the volume of the pre-spore mass (y) varies directly with its ability to deliver S into the anterior region (k_1), and that the volume of the pre-stalk mass (x) varies directly with the utilization of S in the pre-stalk reaction (k_2). That is,

$$y \propto k_1$$

$$x \propto k_2$$

Now in the case of *D. discoideum* there is no stalk formed during migration. Therefore the amount of pre-stalk is completely dependent upon the rate of supply of S. That is,

$$k_1 = k_3$$

$$\therefore \quad \frac{y}{x} \propto \frac{k_1}{k_3}$$

$$\text{or} \quad y \propto \frac{k_1}{k_2} x$$

In other words, the relation of x and y for *D. discoideum* is linear, giving a slope of 1 when x and y are plotted logarithmically. This is consistent with the observed facts. (There is no reason to plot the data logarithmically except for the purpose of comparing it to *D. mucoroides*).

In the case of *D. mucoroides*, which continuously forms a stalk during migration, we assume that the polar factor S is channeled in two directions in the formation of both stalk (k_2) and pre-stalk (k_3). There is therefore less S available for pre-stalk and, accordingly, the pre-stalk of *D. mucoroides* is smaller (as shown in Fig. 2). The relation between pre-spore and pre-stalk volume is in fact an allometric one (as shown in Fig. 3).

Since the slope of the line when plotted logarithmically is greater than 1, we must make a further assumption concerning the relation of the polar factor S to the volumes of x and y. There are numerous possibilities; for instance, we could say that the process of stalk formation in some way causes a nonlinear delivery of S into the pre-stalk zone. That is, the amount of S available for pre-stalk material does not have a linear, but

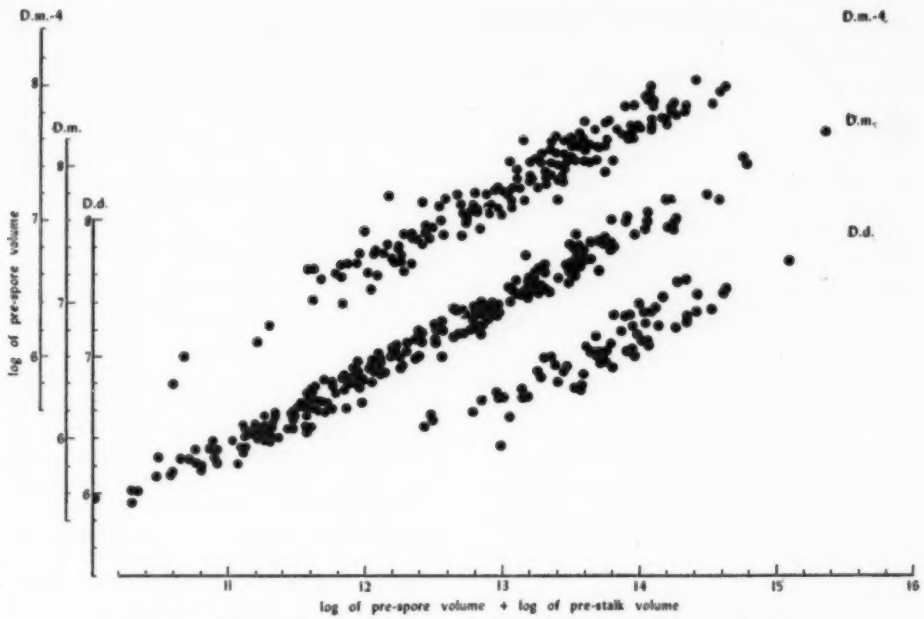

FIG. 9. A LOGARITHMIC PLOT OF THE PRE-SPORE VOLUME AGAINST THE SUM OF THE PRE-SPORE VOLUME AND THE PRE-STALK VOLUME

Reading down the curves are for DM-4, other *D. mucoroides*, and *D. discoideum*.

rather an exponential, relation to the size of the cell mass. But since the details of the mechanism are unknown, it is perhaps only useful at the moment to remember that in *D. mucoroides*, where the stalk is present, there is a reduction in the size of the pre-stalk volume, and that this can easily be interpreted in terms of the proposed polar factor scheme.

In comparing the two strains of *D. mucoroides*, it may be assumed that for some reason in DM-4 the percentage of fast cells is low relative to the total mass. This means that if two cell masses, one of DM-4 and the other of DM-11, are to deliver an equivalent amount of S in the anterior portion, then their anterior portions (x) will be equivalent in size because in both cases the utilization of S will be equal (k_3). From one previously mentioned assumption ($x \propto k_3$) this would result in equal pre-stalk zones (x).

However, we have suggested that in DM-4 the number of cells required to produce this equivalent amount of polar factor (S) is comparatively large. Therefore the volume of the pre-spore areas (y) would not be equal, but greater in DM-4. Since the kinetics of the reactions are in no way affected, one would not expect a change in the slope of the line, but there would be a change in the constant b, which conforms with the experimental results. (It is interesting to note here that the DM-4 strain is somewhat special in its periodic acid-Schiff staining properties. It shows a gradient of staining, with the greatest intensity at the anterior end (as described for *D. mucoroides* in Bonner, Chiquoine, and Kolderie (1955), while the other strains showed a more uniform staining, with an abrupt zone of light cells at the posterior end (see Fig. 2.)

The only case not mentioned is that of *Polysphondylium*. Here, because of some alteration in the timing, some delayed maturity, there is no pre-stalk zone. Therefore all the S is used directly in stalk formation, and there is no division line to measure.

In summary, the theory presented here is that there is a polar factor which is involved directly in the formation of the pre-stalk condition as well as the stalk itself, and that the different proportionality characteristics of different species and strains can be directly accounted for by such an hypothesis. It may now be helpful to consider

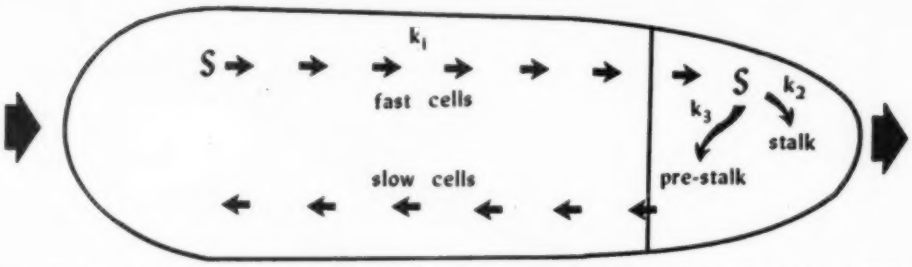

FIG. 10. DIAGRAM ILLUSTRATING THE HYPOTHESIS OF POLAR CONTROL OF DIFFERENTIATION IN SLIME MOLDS

S indicates a polar factor which moves forward at rate k_1 and is used to make stalk at rate k_2 and pre-stalk at rate k_3.

this theory in the light of the evolution of the cellular slime molds.

THE EVOLUTION OF CELLULAR SLIME MOLDS

The first step in considering the evolution of slime molds is to speculate on their adaptive value over free-living amoebae. This step is in many ways the most difficult because we are forced to make the gratuitous assumption that they are adaptively superior; yet there is little or no evidence to show that this is the case. Free living amoebae which are incapable of forming cysts, others which are, and the communal slime molds all live side by side in the soil and must have done so for millions of years.

There are some conceivable advantages to the aggregation behavior of slime molds. For one thing, it may be that by coming together in groups in the very beginning certain deficiencies were masked, and as with syntropism in bacteria, or heterocaryosis in fungi, the pooled resources of a number of cells may have resulted in a sort of mutual dependence. Another point is that, in all cases of cellular slime molds, morphogenesis spatially separates the feeding, vegetative stage from the fruiting, sporulation stage. Feeding, which involves the phagocytosis of bacteria by thin, delicate amoebae, must occur in an aqueous medium. The formation of spores, on the other hand, involves a desiccation of the amoebae, which become encapsulated, and this conceivably could be more efficiently performed in the atmosphere (although many free-living amoebae form cysts in water). More important is the idea that by lifting the mass away from the region of feeding, a process which is abetted by the light and heat tropisms, the spores are in a more favorable position for dispersal. The cellular slime molds would certainly seem to have a more effective method of spreading than free-living amoebae.

With these basic assumptions as a foundation, let us now trace a hypothetical sequence of events from the separate, isolated amoebae to the more complex forms. The first step may have been a sensitivity to certain substances given off by their own kind, which led ultimately to the acrasin-controlled aggregation. Aggregation involves a polar movement of cells and with this polarity comes a gradient: a high activity in the front end of the cell mass which decreases posteriorly.

The next step might have been the production of a pedestal to isolate the spores from the substratum. Relatively solitary amoebae such as *Sappinia* may have individual stalked cells or cysts, but more interesting is the recent discovery by Raper (1956) of the new genus *Acytostelium*. This form has a simple, although not highly organized, aggregation, and the resulting small cell mass rises into the air and exudes an extremely delicate cellulose cylinder that is devoid of any stalk cells. The point is that all the cells produce stalk material and then subsequently they all produce spores; there is no division of labor.

If now, in an *Acytostelium*-like ancestor, there was an increase in variability within the cell mass (and the importance of this supposition cannot be overemphasized), then one would expect the beginning of a sorting out of fast, perhaps high-energy, cells and slow, low-energy cells. With this differential ability to move would come a differential ability to produce or contribute in the stalk or in the spore direction.

One has to imagine that there has been some sort of facilitation in this sorting out, that is, the anterior reaction in particular has become exaggerated, perhaps simply because fuel is now constantly poured on the fire. But the process is so

energetic that the fast cells become virtually consumed; they become incapable of further propagation and contribute their hollow frames to give further support to the stalk they have manufactured. At first there is a continuously variable population of fast and slow cells, but by this facilitation connected with the anterior reaction, the fast cells produce a totally new cell type: the pre-stalk and the stalk cell. Therefore, the continuous variation results in a discontinuous one, for the labor is finally divided into the two functions: spore formation and the morphogenetic activity of stalk formation.

The situation described thus far applies to *D. mucoroides*. *D. discoideum* has made one further, obvious step forward. For organisms that have ceased all feeding before aggregation, cellulose, which surrounds the stalk, is a precious substance. To migrate 100 mm. or more is a great expense in both cells and cellulose for *D. mucoroides*, while *D. discoideum* can cover the same distance without forming any stalk. Therefore, by changing the timing of the various steps that lead to maturity, it has been possible to migrate greater distances more economically.

In many ways *Polysphondylium* presents the greatest enigma. Again, by an alteration of timing, that is, by delaying the preliminary steps toward maturity until the very last moment, this form has been able to produce a fruiting body with many side branches. But here the adaptive advantage seems especially hard to grasp. Perhaps by breaking up the number of sori into small branches the effectiveness of dispersal is increased, but this is an uncertain hypothesis at best.

In conclusion, it might be said that in these proposed evolutionary steps the most interesting advance is the idea that the cell variability within an organism may increase, but always necessarily in a continuous fashion. Then, since the variation involves a polar activity (i.e., polar movement), there is an opportunity for reactions to exist at one end of the cell mass that are absent in the other. Therefore, the continuous variation turns into a discontinuous one, and the result is a division of labor, a differentiation. Furthermore, the fact that there is a balance between the rates of polar movement and the rates of the anterior reaction means that the spacing of differentiation is controlled and proportionality is the result.

SUMMARY

A basic problem in the study of the development of slime molds is an explanation of their proportional development. It has been possible to work out a theory which satisfactorily accounts for the many experimental observations that have been gathered on this subject.

Differentiation begins in the sausage-shaped cell mass, and from previous work it is known that there are certain specific chemical differences between the anterior, pre-stalk end and the posterior, pre-spore end. Furthermore, from new observations presented here, it is now known that these presumptive areas are proportionate in cell masses of different size and even in parts of a cell mass that has been cut into fractions.

Clearly, then, a cell in the anterior end "knows" how many cells lie posteriorly, for if they are removed experimentally the anterior cells accommodate proportionately to the new loss. The theory assumes that this information is carried by a polar movement; in fact, it specifically suggests that certain fast cells are constantly arriving at the tip, and if there is a reduction of the posterior portion then there is a corresponding reduction of these messenger cells.

The "message" carried may be simply a supply of food necessary for a reaction taking place at the anterior end. This anterior reaction is the one which is responsible for the formation of the pre-stalk and stalk condition. In any one species, then, there is a balance between (1) the rate of delivery of the polar factor to the anterior reaction and the rate at which this reaction produces (2) the stalk and (3) pre-stalk portions. Different species and strains have different proportionality characteristics, and these differences could be accounted for by differences in the rates of the three above-mentioned processes.

In considering the evolution of such a mechanism of differentiation, the first step might have been an increase of variability of the cells within the cell mass with respect to their stalk-forming and spore-forming abilities. Since the cell movement in such masses is polar (presumably because of the acrasin mechanism and pull tensions among the amoebae), the fast and slow cells sort out, and such concentration of one cell type has led to a facilitation or an amplification that is the anterior reaction. Therefore, random variability in a cell mass has ultimately, according to this hypothesis, produced a discontinuous, proportionate cell difference that has all the qualities of a controlled pattern of differentiation.

APPENDIX

1. *Modification (for slime molds) of V. R. Gregg's Methylene Blue Technique.* The pseudoplasmodia are fixed for 1 to 2 hours in a solution of 5 ml. of formalin in 95 ml. of 70% ethyl alcohol. The staining is for an hour in 0.25 g. of methylene blue, 100 ml. of 70% ethyl alcohol, and 0.5 ml. of conc. HCl. This is followed by a very short interval in absolute alcohol and then in methyl salicylate, where they remain for 3 to 24 hours. Before mounting in clarite, they are put through a short change in fresh methyl salicylate followed by 5 minutes in toluene.

2. *Summary of the results of the significance tests of the slopes of the lines indicated in Fig. 9.* A formal test of significance of the hypothesis that the slope of the *D. discoideum* curve is 0.5 gives a t value of 0.553. This is obtained by taking the difference between the observed and the theoretical slopes, and dividing this difference by the standard error. Since 0.553 lies between the 80 and the 50 per cent points of the t distribution for 61 degrees of freedom, it is clear that there is no reason to invalidate the theoretical value of 0.5.

In the same way a test of the significance of the hypothesis that the slopes for DM-4 and the other strains of *D. mucoroides* are each 0.5 is again obtained by calculating the values of t, which are found to be 3.21 and 5.89 respectively. Since 3.21 (and hence 5.89) lies beyond the 0.2 per cent point on the t distribution for 180 and 249 degrees of freedom, the data are clearly inconsistent with the hypothesis tested. Therefore, we can conclude that the slopes of the lines for all the *D. mucoroides* strains tested are larger than 0.5.

Finally, it is possible to test the hypothesis that the slopes of DM-4 and the other strains of *D. mucoroides* are the same. The value for t in this case is 0.5689, which lies between the 80 and the 50 per cent points of the t distribution for 180 and 249 degrees of freedom. Clearly there is no basis to doubt the hypothesis that the two slopes are the same.

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CENTRIFUGAL SPECIATION

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INTRODUCTION

MODERN population systematics rests on the assumption that species arise when a parent population is divided into geographical fractions, each isolated from the next by physiographic (or biotic) barriers. During such geographic isolation, the daughter populations can accumulate genetic differences, some or all of which reduce their chances of interbreeding freely and effectively. As soon as these differences accumulate to the point where they constitute a reproductive barrier separating the daughter populations, the latter are then to be considered as newborn species. It must be added that the objective test of a reproductive barrier, and hence of species status, is made only when the daughter populations come into geographic contact. Thus, allopatric populations of obviously close relationship cannot be objectively judged as species or as less than species in the absence of information on their interbreeding reaction. This is the vexing *uncertainty principle* of systematics (Brown and Wilson, 1956).

Geographic separation of populations into potential and then actual species is often assumed to have followed one of two principal patterns.

I. The parent population is split by the intrusion of some feature, usually physiographic, that interferes with breeding between the resulting daughter populations. Barriers usually cited are glacial tongues, zones of aridity, arms of the sea, mountains, areas of high volcanic activity, and the like. We may call this geographical isolation by *division*.

II. The parent population is limited by physically or biotically unsuitable regions that ordinarily prevent its spread. However, under unusual circumstances, a propagule from this population may cross the external barriers and reach a new area favorable to its establishment and subsequent increase. Once the daughter population is safely launched in its new home, its isolation from the parent population may for a time be complete. This process we shall call isolation by *colonization*.

Both of these kinds of geographical separation are frequently invoked to explain the present distributions of species groups, superspecies, and the populations comprising the so-called polytypic species. There can be little doubt that populations are split by such means, or that the result is often a species separation. But it may be a mistake in emphasis to think of these simple processes by themselves as the kinds of species-division most fundamentally important in evolution. It should be questioned that isolation by simple division alone can account for all the overlapping complexities of many continental faunas, or the species swarms in ancient lakes, for instance.

The generally feeble, adaptive, and counter-competitive potential of colonist endemic species on islands (especially when confronted with changes in biotic environment and with new competition) is well-known. It is necessary to question the hypothesis (e.g., Mayr, 1954) that insular faunas may be important potential foci of new major-group evolution, as well as the opinion that species which have evolved on offshore islands as colonists from mainland stocks may ordinarily reinvade "empty niches" on the mainland. The evidence provided by P. J. Darlington (1948, and in press) indicates instead that insular situations are more often in the nature of evolutionary cul-de-sacs, from which there is little chance of important return traffic of species that have been in residence there long enough to have evolved into island endemics. The elaborately radiated geospizine finches of the Galapagos and the drepaniids of the Hawaiian Islands, already showing a rather high incidence of contemporary extinction among their species, can only be considered representative examples illustrating adaptive fragility in insular complexes.

By deprecating the relative importance of simple division and simple colonization as speciation processes, we inevitably raise the question of some other possibilities. One of these alternatives looks so promising that most of the rest of this paper will be spent in discussing it. I refer to the

idea that species formation proceeds through a centrifugal progression of variation, and to the supplementary proposition that the process requires density changes and consequent expansions and contractions of geographical range of the evolving population in order to reach completion. Elements contributing to this hypothesis have been both tacitly and openly recognized for many years; some of them are probably as old as the concept of organic evolution itself. I may mention as prominent among contributors to related aspects of "centrifugal theory" Willis (1922), Matthew (1915), Vavilov (1926), Timoféeff-Ressovsky (1940), and P. J. Darlington (1948). There are many others.

So far as I am aware, no one of these authors has dealt with more than a part of what will follow shortly as my hypothesis, and some of them were thinking primarily about the rise and spread of major taxonomic groups, not about the origin of species. Nevertheless, their writings are an indication of a strong and continuing interest in evolution viewed as a central-peripheral succession of taxa. I therefore regard the hypothesis as only the particularized expression of a concept long latent in evolutionary thinking.

THE HYPOTHESIS

The maximum geographical range attained by a species over an indefinite period of time includes areas favorable and also unfavorable for its continuous breeding and increase. Within the maximum range, the populations of the species normally undergo successive expansions into the less favorable peripheral areas, alternating with contractions into more favorable refuges. The expansions and contractions are the sequelae of inevitable density fluctuations affecting all or part of the species at one time. The more important genetic changes tend to be incorporated in the central populations, and are carried outward with these during the phases of expansion. With the phases of contraction, populations of the species disappear from the peripheral areas, except in relatively restricted refugial pockets or islands that are favorable enough to allow survival of some expansion-phase remnants. At this stage, of course, the central populations are geographically isolated from the peripheral remnants, permitting the expected accumulation of genetic differences between them. If, as must happen in only a small proportion of cases, the differences mount to the point of reproductive isolation, the next phase of expansion will establish the geographical contact needed to confirm the new species difference. The new, contiguous, or overlapping species will likely be forced to avoid hybridization (through reinforcement of the reproductive barriers) and competition (through ecological or geographical displacement). The chances are that in most such contacts, the "new central" species will overwhelm the "old peripheral" species by competitive pressure, or, more likely, by means of adaptations of the general "aggressive" type, functioning to remove or incapacitate competitors. But if the two new species can specialize to divide the exploitable environment between them, they may both persist.

The most significant parts of the hypothesis are the emphasis on the center as the principal source of evolutionary change leading to "potent" new species and higher categories, and the role of population density fluctuations in spreading characters and making and breaking the contacts between populations.

ARGUMENT AND EVIDENCE

The maximum geographical range attained by a species over an indefinite period of time includes areas favorable and also unfavorable for its continuous breeding and increase. The truth of this observation is so obvious that we shall not spend time discussing it at length. It should be pointed out, however, that *favorable* areas differ in extent. Other things being equal, the favorable areas of greatest extent should be *most* favorable for the continuing existence of the species, merely because they support the largest total populations year after year.

These populations should have the best chance to originate successful new types through mutation, recombination, chromosomal transformations, gene dispersal, and interdeme selection. The nature and interactions of these processes are the concern of population genetics and are largely outside the scope of this paper. The results of the processes are here generally lumped under non-committal terms such as "character," "genetic change," and so on, and in many cases, this conveys all that is known about them genetically. Whatever their genetic basis, most characters seem to be either directly or indirectly adaptive, so that an area with many exploitable niches available should tend to favor and maintain their variation. The favorability of an area for a given species may indeed be largely a

matter of how many niches it includes that are open to the species (Dobzhansky, 1951). At any rate, it seems clear enough that the largest continuous or near-continuous favorable area of a species range is at once the most dependable refugium of a species and the chief fountainhead of its store of variation and general adaptive improvement. Such an area constitutes an *evolutionary center* for the species.

One might expect variation generally to increase from the periphery of the range going inward toward the most favorable areas. However, information on this subject is disappointingly scanty in the literature, probably because the most variable characters are usually of little interest to taxonomists (but see Reinig, 1939; da Cunha, Burla, and Dobzhansky, 1950).

The evolutionary center is, of course, not necessarily coincident with the geographical center of the species range, or with the center of its particular home land-mass. In Asia, North America, and Australia, a large number of species of animals find their optimum situations in the mild, moist eastern parts of those continents, but their ranges often extend far out into the less hospitable central and western reaches of their respective continents. In Africa and South America, the climates most favorable to animal life in general, and thus supporting the largest number of individual evolutionary centers, happen to be near geographical centers of these continents. In such circumstances, geographical patterns of evolutionary change are more free to develop symmetrically in all directions.

In addition to the main evolutionary center, other "permanent breeding areas" may constitute subcenters of varying importance, depending upon their areal extent and the degree of their favorability. These are of lesser importance, since their chances of evolving superior general adaptive types are limited by their smaller resources of variation.

Within the maximum range, the populations of the species normally undergo successive expansions into the less favorable peripheral areas, alternating with contractions into more favorable refuges. The expansions and contractions are the sequelae of inevitable density fluctuations affecting all or part of the species at one time.

The journals have accumulated an endless amount of data to show that particular animal species have increased or contracted their ranges within historical times, or even over the span of a few years. Usually these records cover the advance of the most conspicuous or noxious of animals, while the corresponding retreats are, as has already been mentioned, seldom the subjects of documentation. When it comes to determining causal factors behind expansion or contraction, the literature is still less satisfactory. Expansion is most often linked, however uncomfortably, to climatic amelioration, while the arch-destroyer, *Homo sapiens*, is too readily invoked as the cause of range contractions.

In the surprisingly scarce instances where reasonably complete and detailed records are available on expansion-contraction cases among animals, one often finds evidence of density-conditioned processes at work. In general, it seems that animals usually emigrate from "favorable" territory into ordinarily less favorable areas only, or most actively, when population density in the "favorable" or "central" territory threatens to reach a threshold status with respect to some life requisite of the species, such as food. The emigration often appears to be initiated directly by proximate mechanisms that are distinct from, but normally associated in some way with, the ultimate effect having survival value for the population or species (Lack, 1954). In other words, dilution of the central population through emigration may normally be triggered by an incidental density effect, such as physical crowding, or by the interference of an external condition normally accompanying requisite shortage, such as drought. The ultimate effect is to damp increase at a crucial time, checking in advance the last-straw generation that could deplete all of the species requisites and cause a disastrous population crash.

The famous "irruptions" of lemmings, of birds such as the crossbill, and of insects such as plague locusts and the California oak moth provide much studied but by no means unique examples of animals that react to increasingly dangerous density conditions in favorable evolutionary centers by emigrations en masse. Whether most or all animal species "normally" tend to show similar reactions to density increase is of course an unanswered question, and one crucial to the present hypothesis. This question can be answered only by accumulating the proper observations.

In the lemming, mass emigration either precedes or accompanies food shortage, but the proximate cause of emigration in individual lemmings is not yet well understood. Perhaps "derangement" of

the type found by Chitty in crowded *Microtus* voles is relevant to the lemming situation. It is interesting to note that emigrant lemmings sometimes establish new colonies beyond the central range (summary in Lack, 1954).

The crossbills are a principally holarctic group of finches, all specialized feeders on the seeds of conifers. Three species are generally recognized (*Loxia curvirostra*, *L. leucoptera*, and *L. pytyopsittacus*), but some of their many "races" may actually be biological species. Most of the populations are given to wandering in search of good cone crops (which are very irregular), and their places as well as seasons of breeding may differ widely from year to year (Griscom, 1937).

From time to time, one or more of these forms engages in a mass irruption that carries large numbers of birds, particularly juveniles, far beyond their usual breeding ranges, and even to remote islands at sea. There is sometimes a smaller return movement, but this usually seems insignificant by comparison with the outward one. The irruptive movements are made in a heightened state of excitability resembling that of the flocking of true migrant birds on the point of exodus, and there are observations to suggest that population densities are more than usually high in the source areas of the irruption. After reviewing the information available for crossbills and several other birds, Lack (1954) concludes that the major irruptive movements are probably initiated proximately by stimuli associated with crowding, and that the ultimate cause is food shortage.

In other words, one can say that in these birds, emigration from the large favorable areas at the distributional center is both density-conditioned and automatically repeated. It seems very significant that crossbills have been established as permanent breeding populations at several remote extralimital points. It will be profitable to return to the discussion of these colonies later, when we take up the subject of geographical variation.

In a discussion of the phase theory of locusts, Key (1950) shows that in grasshoppers and locusts of several genera in different parts of the world, emigratory outbreaks occur, originating in permanent "outbreak areas," regions that are the true continuous-breeding ranges of the respective species. When thoroughly mapped, such an outbreak area may prove to consist of one or two large, central continuous areas about which are grouped smaller ones at varying distances (e.g., Key, 1938).

Density increase in the outbreak area leads to a mutual stimulation among the insects which finally results in the mass emigration of all but a few individuals into surrounding regions where, according to the species, they may either settle or merely feed and move on.

Migratory locusts normally show a transformation in phase, or morphological type, affecting color and structural characters. Frequently, swarming populations will contain largely phase *gregaria;* dilute sedentary populations, phase *solitaria;* and populations in transitional stages, phase *transiens*. But phase condition is mediated by proximate factors of the environment that are in part, at least, different from those chiefly responsible for causing actual emigration. Therefore, phase is not necessarily always well correlated with the condition of the population as regards actual swarming or non-swarming status. Key considers that the function of phase *gregaria* is to intensifiy the effects and coordinate the events leading to swarming.

> . . . there is evidence that transformation into phase *gregaria* has a quantitative effect upon migration which is probably important in connection with outbreaks, at least of some species. Thus it probably makes migration more general among locusts of an outbreak area. It also induces migration before the available food in the outbreak area is consumed, and maintains the migratory urge irrespective of the food supply in the invasion area. The evidence suggests that the phase *solitaria* migrates mainly, perhaps only, when conditions have become unfavorable.

In a most interesting study of the California oak-moth (*Phryganidia californica* Packard), Harville (1955) demonstrates definite, causal correlations between density increase and emigration operating in both the larval and adult stages. The oak-moth females lay their eggs as near the center tops of the oak crowns as possible. The hatching larvae feed for a time in the adjacent foliage, but as they grow, they tend to exhaust the more succulent leaves, which they normally choose by "sample-and-reject" foraging behavior. As they sample more and more leaves, they gradually move outward to the tips of the branchlets, where they exhaust the food supply and finally lower themselves on silken strands. Upon touching a lower branch, they again forage outward and again repeat the descent by silk thread, finally, if

the food supply in their path is exhausted, reaching the ground. On the ground, the larvae head off randomly and ascend any object in their way, which for some of them may be the very tree they have just left. After their ascent, the larvae repeat the performance, descending stepwise in their set fashion as the shortage of food drives them, until they either die or get enough nutriment to pupate. In light infestations, however, the larvae may complete their development without leaving the tree upon which they hatched.

The adult females are weak fliers. In seeking a place to oviposit, they are attracted to the upper central portions of oak trees in good foliage, and if such trees are available close by, they will not attempt to travel farther. But if the local oak trees are badly defoliated, the females will avoid them and flutter about rather aimlessly in other directions. Their weak flight renders them particularly likely to be borne along on the wind, and it is chiefly by this means that new colonies are started at distant points.

The oak-moth populations apparently never survive the winter in northern California, and frequently do not in the middle part of the state, though some few favorable localities here may normally support overwintering populations every year. In southern California, one of the two or three larval generations overwinters year after year, and these "central" populations presumably furnish a proportion of the propagules that annually make the colonial starts farther north in the depopulated areas.

So far, only the somewhat "peripheral" populations in the middle part of the state have been closely studied by Harville. These suffer drastic crashes every few years during severe winters, and Harville emphasizes his belief that the eventual replacements building up in the depopulated areas are essentially new populations for these areas.

An interesting case of probable density-reactive emigration is reported by R. L. Chermock (1946) and Nielsen and Nielsen (1950) for the pierid butterfly *Ascia monuste*. This butterfly is widely distributed in the New World tropics, and its permanent breeding range extends to Florida, where it shows seasonal density fluctuations. There is also a drastic longer-term fluctuation occurring irregularly every few years, as judged from observed density of the adults. There seems to be little question that the conspicuous northward and westward emigrations of *A. monuste* are correlated with the higher density peaks. However, the larvae, even during adult population peaks, may have an excess of their normal food-plants within reach. Chermock considered that the proximate point of shortage was the adult food, nectar secured from flowers that seemed to him too scarce to supply all the adults in a given area at once during density peaks.

Chermock's observations were limited and rather casual, but his suggestion that nectar for the adults, and not larval food supply, may be the limiting factor that touches off emigration, should at least serve as a warning to those who consider only "obvious" requisite supplies. *Ascia monuste*, like many another mass emigrant, seems prone to establish colonies outside its permanent breeding range. It also makes conspicuous southward migrations in the southern part of its range in Uruguay (T. Eisner, pers. commun.).

The examples cited above are, I believe, representative of what happens, usually in less spectacular fashion, in a great many if not most animal species. Readers will undoubtedly be able to call up additional instances from their experience in field, laboratory, and literature, and it is here urged that data bearing on emigration be more frequently committed to print.

However, it must be said that opinion is certainly not unanimous on the general importance of the causal relationship between density increase and emigration. Andrewartha and Birch (1954), for instance, ask whether emigration phenomena interpreted as being density-dependent are not often just the normal, proportionate dispersal activities of individuals in any population, rather than the disproportionate tendency to emigration postulated for populations that reach critical densities. Considering the strength of the evidence available in favor of density-conditioned emigration as a common occurrence, the objections of Andrewartha and Birch do not seem to me to offer great difficulty.

Their own favorite example, that of *Thrips imaginis* Bagnall populations in South Australia, is invoked as a case in which observed movements of the animals can be explained without recourse to density-reactive emigration. However, this study seems to me to require confirmation and amplification through additional studies of the total natural history of this species. *T. imaginis* is a very widespread species, the main range of which lies in warmer and more constant climates; the species is

known from widespread localities in eastern Australia, New Caledonia, and the Philippines, where it is often abundant (L. J. Stannard, letter, 1956). From this information, it would appear that *T. imaginis* may be existing in South Australia under marginal conditions, and that it may even possibly have been introduced by man. A study of populations in the Philippines or elsewhere in the tropics is clearly called for.

The remarks Andrewartha and Birch make (pp. 123–124) concerning mammal and bird dispersal appear to contain some confusion of proximate and ultimate factors affecting emigration. Their virtual dismissal of mass emigration as an important factor in range extension and extralimital colonization also seems ill-considered considering the evidence available.

The argument over the relative importance of density-reactive influences, and particularly of competition, completely dominates the field of population dynamics today. No two authorities hold exactly identical views, but there is a rather definite division of authors into two opposing schools, one of which (Nicholson, 1954; Lack, 1954) tends to regard competition and density-reaction in general as highly important, while the other (Andrewartha and Birch, 1954; Thompson, 1956) minimizes the significance of these forces My opinions fall closest to those of the first school, provided we can agree on a definition of "competition" that excludes the elements of aggression, dispersal, and adaptation—all of which are seen as *means by which an animal can avoid or reduce competition*, not intensify it (Brown and Wilson, 1956).

Both schools happily recognize that some kind of density fluctuation is a nearly or quite universal quality of populations of animals. The fluctuations can be regular or irregular, and their proximate causes numerous and varied, density-reactive and/or non-reactive. Still, it seems clear that if non-reactive factors assumed to cause all or most of some particular fluctuation are somehow excluded, density-reactive factors in the form of competition will step in to govern populations (Nicholson, 1954). In this sense competition is the ultimate density homeostat, capable of maintaining fluctuation even if other forces fail in this. For our present purposes, we are interested only in satisfying ourselves concerning the inevitability of density fluctuation, however it may be generated.

The more important genetic changes tend to be incorporated in the central populations, and are carried outward with these during the phases of expansion.

I have already made brief mention of the connection between the large, favorable central areas of a species distribution, the prevailingly large breeding populations these will support, and the greater probability that such large populations will give rise to successful new types. This relationship can be supported on wholly theoretical grounds. I believe that it is also reflected in actual data, drawn chiefly from the literature of geographical variation.

We shall take theoretical consideraions first. The genetic changes that mean novelty within a species are introduced at different points in the range, and if they are adaptive, they spread outward from these points. Even if we assume that the range of a species is uniformly favorable, it can be shown that new characters will in one important way have a better chance of arising nearer the center. If we draw a big circle (Fig. 1) to represent the uniformly favorable range of a species, we can place within this some smaller circles to stand for areas over which particular genetic changes (A′, B′, C′ . . . .) have spread. The smaller circles are all drawn at the same size, though of course they would normally vary greatly according to the varying ages and adaptiveness of the characters in a real situation. Since the available evidence indicates that characters usually tend to be distributed without concordance in natural species (Wilson and Brown, 1953), the small circles are spaced evenly. The overlaps (intersects) among the circles, then, represent parts of the range in which the local populations (demes) carry more than one of the changes. The area of heaviest multiple intersection will carry a deme different by a large number of characters from demes of areas where little or no intersection occurs. (See S. Wright, 1956, for related thoughts on "interdeme selection.")

For the simple reason that there are no centers of character dispersal outside the species range, there exists an outer zone of this range in which intersects will be less frequent than they are closer to the center. (The width and distinctness of the peripheral "zone of intersect rarity" depends on the radius of the character-range circles. The smaller the mean radius of these circles relative to

the radius of the whole species range, the more clearcut will be the outer zone.)

From these considerations, it follows that, even in a uniformly favorable species range, the more peripheral demes will tend to be similar among themselves, and individually will differ most from the demes at the very center of the species range. When we apply this concept to real species ranges, the differences in favorability of the included areas should greatly magnify the central-peripheral contrast, provided that other factors do not interfere.

Of course, other factors *do* interfere. When central populations disperse, for instance, they tend to overrun and swamp the peripheral ones, and this process certainly normally opposes central-peripheral differentiation in a most direct and effective way. But even complete swamping of peripheral populations does not mean the total instantaneous disappearance of all peripheral traits. In fact, the persistence of peripherally distributed characters in species ranges now either continuous or discontinuous is good evidence for the central origin of new changes, as is clearly shown by the case of the fire ants, discussed farther below.

We can now examine some cases of variation that appear to follow a central-peripheral pattern. These are drawn from the literature of geographical variation, a literature now very voluminous, and fast increasing. Unfortunately, very many papers that are claimed to deal with geographical variation actually devote most or all of their space to the diagnosis and discussion of so-called "races," subjective entities that serve as much to camouflage as to reveal the variation of individual characters.

I have been forced to draw in the main from the pitifully small minority of papers that do in some measure follow the whole variation in space of individual characters taken separately. There are indications that this documentation could be heavily augmented from examples that are only crudely hinted in the current standard subspecies treatments.

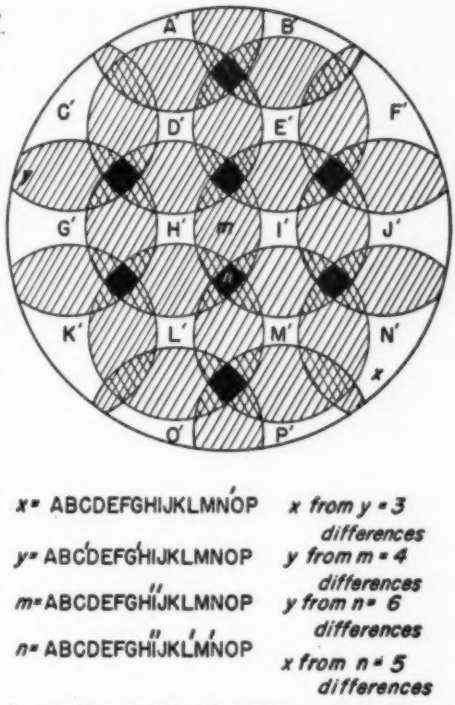

FIG. 1. DIAGRAMMATIC REPRESENTATION OF VARIATION WITHIN AN IDEALIZED SPECIES RANGE

The large circle represents the whole ecologically uniform range of an evenly distributed species population. The smaller circles, marked at their centers by primed capital letters, represent new characters (of the "all or none" type) that have arisen and are spreading at the expense of their respective "normal" versions, assumed to occupy the remainder of the range. Depth of shading indicates the number of new-character circles participating in each overlap. The lower-case italic letters (*m*, *n*, *x*, *y*) are arbitrary sample points chosen to represent demes carrying the character combinations occupying these parts of the range. The letters are used to construct representative character-combination formulae, by means of which the interdeme differences can conveniently be compared. In the formulae, the capitals without primes of course represent the "normal" version of each new character.

The Barn Owl in Europe

Voous (1950) deals at length with the variation of the barn owl (*Tyto alba*, particularly the male) in the eastern palearctic region. Light-colored populations with sparsely spotted white breast predominate in Britain, western France, Spain, North Africa, peninsular Italy, the southern Balkan Peninsula, and on the Mediterranean islands. In central and northern Europe, darker birds are the rule, with more spots on a darker breast background. In the zone between the predominantly dark and predominantly light populations there exist all degrees of intermediacy between the two extremes, both in the relative frequency of light and dark forms at a given

locality and in the development of the several independent characters that are involved in the difference. Thus, we have predominantly dark central populations grading out to predominantly light peripheral ones.

Voous notes that the dark condition is apparently spreading outward and that it "dominates" the light condition at the expense of which it spreads. He thinks that the intermediate populations are "hybrid" in origin. The barn owl is a practically world-wide and notoriously variable bird, and it would be interesting to see Voous' analysis extended to the rest of the populations.

Four Cases among the Drongos

Among modern monographs of bird groups, Vaurie's impressive revision of the drongos (Dicruridae) (1949) is rich in data that suggest centrifugal dispersal of characters in the more widespread species.

In one superficially simple case, the African drongo (*Dicrurus adsimilis*) occupies nearly the whole of Africa south of the Sahara. The Congo populations (race *coracinus*) have the mantle and underparts "velvety," and their immatures have indistinct or no light-colored barring beneath. The remainder of the range is taken up by more glossy birds having immatures whitish-barred beneath (race *divaricatus*, northern; race *adsimilis*, southern). Around the velvety Congo population, and between it and the surrounding glossy populations, has been found a broken ring of intermediate samples (race *atactus*) extending even to Principe Island in the Gulf of Guinea (race *modestus*). However, this "intergrade ring" is unusual in its very discontinuous range, and perhaps it is in part merely the reflection of a character displacement system. The velvety and glossy populations meet in some places at the eastern end of the Congo without intergrading. This case needs further study, but whether the velvety and glossy populations are eventually found to belong to the same or to different species, it does seem possible that they conform to the pattern of a central character replacing a peripheral one.

In the Oriental ashy drongo (*Dicrurus leucophaeus*) Vaurie recognizes fifteen geographical races, differentiated mainly on general darkness of plumage color and presence and/or development of facial white marks, but also on general body size and proportions of wings and tail. I have reproduced Vaurie's map (Fig. 2) showing the distribution (by "racial averages") of the two outstanding character variations. It seems to me that the distribution of these characters forms three roughly concentric groupings. At the center, in India and tropical southeastern Asia, there are dark and medium gray populations without white facial markings. Beyond this, an arc of separated populations varies from light gray (northern China) to medium gray (Sumatra and Mentawei). This arc is marked by the decided development, especially at its most remote terminal portions, of whitish facial markings. The third, outermost ring of population is still more widely scattered, occurring on Palawan and nearby Balabac; Java, Bali, and Lombok; and Simalur, off the western coast of northern Sumatra. These populations are medium gray, without white facial markings, and are so similar among themselves that Vaurie (who cannot be called a conservative in the matter of recognizing races) was led to assign them all to a single race, nominate *leucophaeus*.

It is, of course, possible that the characters marking each of the isolates forming the outer rings arose independently (i.e., are polytopic). Another possibility is that the whole pattern marks successive waves of characters spreading outward from the continent. Even the alternation of characters (face unmarked—face with white markings—face unmarked) may be significant, as will be discussed below for the crossbills.

In the greater racket-tailed drongo, *Dicrurus paradiseus*, the birds from India, Burma, and southern China have long, flowing frontal crests. The crest shortens toward Ceylon and toward Sumatra in the south, and finally disappears in the populations on Borneo. On small islands in the south China Sea, in the Andamans, and in Sumatra and Malaya, the crest is absent in varying proportions of the samples available.

Vaurie thinks that the species *D. paradiseus* originated in Borneo, presumably chiefly because the least specialized race occurs there, and that it then moved northward and westward into Asia, producing specialized crested forms at the extremes of its range. In my view, the pattern shows that something like the opposite may have happened. Specializations have arisen on the mainland and are travelling outward *toward* Borneo. In the map (Fig. 3), we see them in mid-passage.

In the spangled drongos (*Dicrurus hottentottus*) there exists an enormously complicated taxonomic picture that may in some respects illustrate cen-

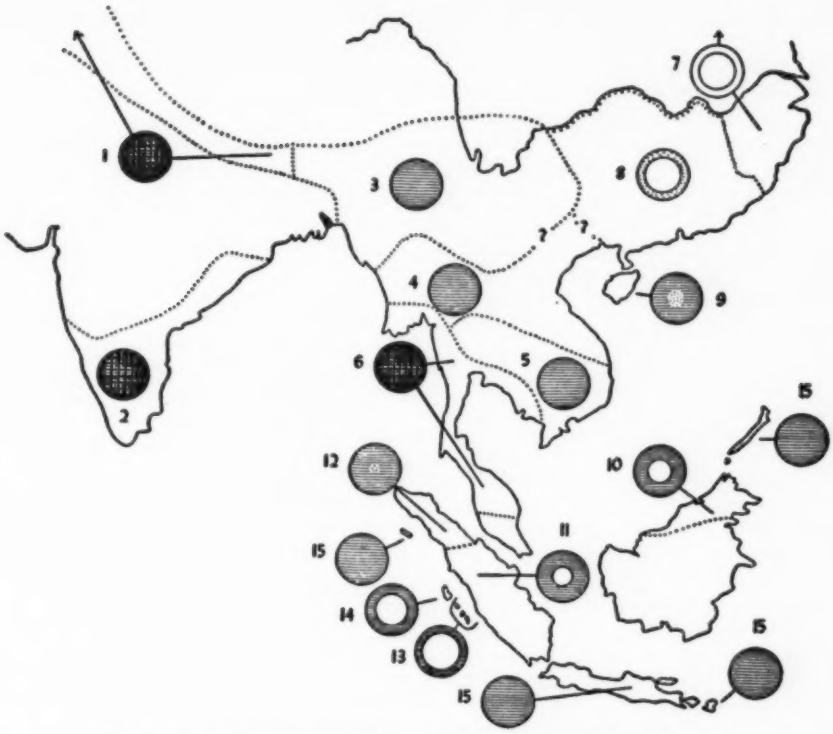

FIG. 2. COLOR VARIATION IN THE ASHY DRONGO, *DICRURUS LEUCOPHAEUS*

The relative degree of general plumage darkness is shown by the full or outer circle, and the relative development of the white facial mark, where present, by the inner circle. Each of the races recognized by Vaurie is represented by a different number. (After Vaurie, 1949.)

trifugal migration of characters. Vaurie's arrangement allows for three groups or "waves" of races, group A being the oldest and most primitive in general character, group B next oldest and derived from A, and C the final, most specialized wave. Group A is the most remote from the Asian mainland, ranging from the southern Philippines through the Moluccas, Melanesia, and northern Australia. Groups B and C replace each other in different parts of the East Indies, C extending onto the mainland of southeastern Asia as far as northwestern India and China. If one considers alternatives to Vaurie's belief that the place where the most generalized races are now found (southern Philippines, Moluccas) is the ancestral home of the species *hottentottus*, the possibility can be entertained that the three waves are centered on southeastern Asia, and that this is the present chief focus of evolution for the species. In view of the findings of Inger (1954) and P. J. Darlington (1948, and in press), it would seem that in other vertebrates the Philippines are more often a zoogeographic terminus than a source of stocks able to expand vigorously to large areas outside these islands.

The distributions of the Asiatic drongos are paralleled in simple fashion by the two very closely related ants *Stictoponera menadensis* (Celebes, Borneo, Philippines) and *S. bicolor* (Southeast Asian mainland). These overlap on Sumatra and Java, and they may not even be specifically distinct (Brown, 1954).

Some Other Birds

Clancey (1955) gives an interesting summary of geographical variation in the orange thrush,

FIG. 3. VARIATION IN THE CREST OF THE GREATER RACKET-TAILED DRONGO, *DICRURUS PARADISEUS*

The numbers refer to the races recognized by Vaurie. The Javanese race *formosus* appears to show a reversal of the clinal trend toward loss of the crest shown by race *platurus* (no. 4) of Sumatra and Malaya, but this is misleading. Most Malayan and apparently at least some southeastern Sumatran samples have the crest about as large as in the Javanese populations; crestlessness is more characteristic of the northwestern Sumatran birds and those from the western Sumatran islands. Treatment of these populations as a single race tends to conceal the very interesting heterogeneity of crest development they show. (After Vaurie, 1949.)

Turdus gurneyi Hartlaub, of eastern and southeastern Africa. This thrush is divided into seven "races," each completely isolated from its neighbors by unfavorable territory, and strung out in line along the highland forests from Mt. Kenya south to Pondoland. He treats these isolates as races, though some or all of them could be distinct species from the data presented. However, it seems reasonably clear that they are closely related membrs of a single stock.

Though we are given only the conventional "race by race" analysis, it is possible in this case to gain a crude idea of some of the independent character variation, especially when Clancey summarizes, and in reference to his map:

> From the discussion on the characters shown by the different populations of *T. gurneyi*, it is concluded that seven racial divisions can be recognised to advantage

in our taxonomic arrangement. *T. gurneyi* would appear to be a species of tropical origin which penetrated far into southern Africa during a dispersal optimum, when suitable forests were more extensive and less fragmented in their distribution than at present. This supposition is supported by the fact that adults of the nominate race, which consists of the southern terminal populations, are completely without cinnamon on the rump and upper tail-coverts, though this character is present in the juvenal state, whereas all tropical forms of the species have this salient plumage character in varying degree in the adult plumage. But the new knowledge that the northern and southern terminal populations are larger dimensionally and have larger white wing-spots than those of the five interposed forms, all of which have markedly shorter tails, complicates the preparation of any valid distributional history for the species at the present juncture.

The three characters by which the terminal races differ from the central ones (judging now

only from Clancey's data) are the kind of variates that could be allometric in their expression; in other words, variation in size of the white wing spots and in tail length may be tied to general body size, in which case, of course, the characters cannot be considered "independent." If in this case any two, or all three, of the characters are really independent, however, their peripheral distribution would seem even more significant than it does when they are conservatively treated as a single character.

Lack (1953) reviews the geographical variation of the European robin (*Erithacus rubecula*). In central and northern Europe, the robin has a grayish back and a rather pale reddish breast. In some outlying parts of its range, in Britain, the central Canary Islands, Tunisia, and Persia, the birds have a more brownish or olive back, and the breast color becomes a more intense orange-red. The more richly colored peripheral populations are joined to the central continental populations by intermediates in intervening continental areas, although it is clear that the back color and breast color show poor overall concordance in these areas. Except for the central Canaries, the Atlantic islands (Azores, Madeira, western Canaries) all have the pale continental kind of bird at the present time, perhaps a sign that this form is spreading.

A circumpolar passerine, the Lapland longspur or Lapland bunting (*Calcarius lapponicus*) apparently varies clinically (in bill size and lightness of color) both eastward and westward from Greenland, toward Alaska on one side, and toward Europe and Siberia on the other (Williamson and Davis, 1956).

During the autumn in 1953, a strong irruption of these birds reached Scotland and Norway. Judging from the average larger bills and darker color of these birds, as well as from strong meteorological evidence, Williamson and Davis find the emigrants to have originated in the Greenland area. An exceptionally strong influx of this species also reached the southern United States during the winter of 1953–1954, presumably from the arctic areas to the north. This all suggests that population densities in Greenland and the eastern Canadian Arctic were high in 1953, and that a mass emigration in at least two directions derived from this circumstance. There appears to have been no return migration of similar scope in the Scottish area during the spring of 1954. Scotland, Norway, and the United States usually receive migrant Lapland longspurs each winter in much smaller numbers, apparently from Greenland and neighboring American arctic areas.

It is interesting that in this longspur the chief source of at least one major irruption, and also of annual small-scale dispersal movements, should correspond generally so well to the apparent center of observed variation.

The Meadow Frog

The important study by Moore (1944) of variation in the meadow frog (*Rana pipiens*) in eastern North America shows not only that individual characters vary independently and discordantly, but that some of them vary more or less on a central-peripheral plan. The patterns are never exactly the same, of course. The external vocal sacs of the male, for instance, are predominantly well-developed in samples from southern New York and Indiana south to Florida, Louisiana, and Oklahoma. External vocal sacs are usually rare or poorly developed in the northeastern states, Quebec, and in most of the states west of the Mississippi River, including Texas.

Moore's map of the distribution of males with and without oviducts (Fig. 4) shows the pattern typical for a "dominant" and expanding character. In the central part of this sampled area, all male meadow frogs examined lacked oviducts. In the peripheral areas in the west, northwest, north, northeast, and in peninsular Florida, most males have oviducts. However, occasional samples taken in these outer areas do lack the oviducts. Such evidences of incipient swamping of peripheral by central characters are commonly seen in central-peripheral variation.

A Brazilian Legless Lizard

The exhaustive study of the South American lizard *Amphisbaena fuliginosa* by Vanzolini (1951) is a model work that all students of variation would do well to examine. The samples are drawn from widespread localities in the northern half of South America and Panama. Seven diverse characters are studied independently, each for the entire range, and an attempt is made to synthesize the conclusions. The final result is the delineation of five "races," but in my opinion these add nothing to the very thorough basic analysis, and they would probably be misleading if taken without it.

The variation of the seven characters is discordant and uneven for the most part, but two of

FIG. 4. DISTRIBUTION OF MALES OF THE MEADOW FROG, *RANA PIPIENS*, WITH AND WITHOUT OVIDUCT

Samples are from the United States and adjacent parts of Canada only, though the meadow frog has a much wider range in North and Central America. Each dot or circle represents 1 to 4 male frogs dissected; those in Vermont, New Jersey, and Long Island represent much larger samples. (After Moore, 1944.)

them do seem to show a rough sort of agreement in their distribution. These, number of body annuli and relative length of tail, follow strongly central-peripheral patterns. The body annuli (Fig. 5) show high counts in the area of Manaos, and drop off from this in all directions, most rapidly toward the northwest (Colombia and Panama). An arc of similar counts stretches from Peru around the northern Brazilian border to the Guianas and Trinidad.

The tail-length variation is strikingly similar in most details to that of the annuli, but here the central Amazonian values are low, and those surrounding are higher. Considering all characters together, Vanzolini finds that the Peru-Ecuador (*"bassleri"*) populations are more like those of the Orinoco-Guianas area (*"fuliginosa"*) than these are like the intervening Amazonian populations called *"amazonica."*

> . . . although *A. f. amazonica* has a range situated between those of *bassleri* and *fuliginosa*, its characteristics are not intermediate between those of the named forms. On the contrary, *bassleri* and *fuliginosa* are very closely related forms, differing chiefly in color.
>
> This situation could have arisen in two ways: (a) *amazonica* giving rise to two convergent forms in different parts of the range; (b) *amazonica* being the result of the evolution of a population occupying the central part of a territory, on the fringes of which the primitive stock suffered further but less extreme differentiation.
>
> If we consider now [the Colombia-Panama and eastern Brazilian populations] we see that they approach more closely the forms with low counts of body annuli (*bassleri* and *fuliginosa*) than *amazonica*. In this manner I believe the second hypothesis listed above is the more probable. . . .

The New World Fire Ants

In the cosmopolitan ant genus *Solenopsis* the most notorious pest species are the members of the neotropical *geminata* group (subgenus *Solenopsis*). *S. geminata*, a species whose original range lay in the circum-Caribbean countries, has spread widely over the tropics of both hemispheres. *S. xyloni*, a widespread southern nearctic species, appears largely to have been replaced by *geminata* along

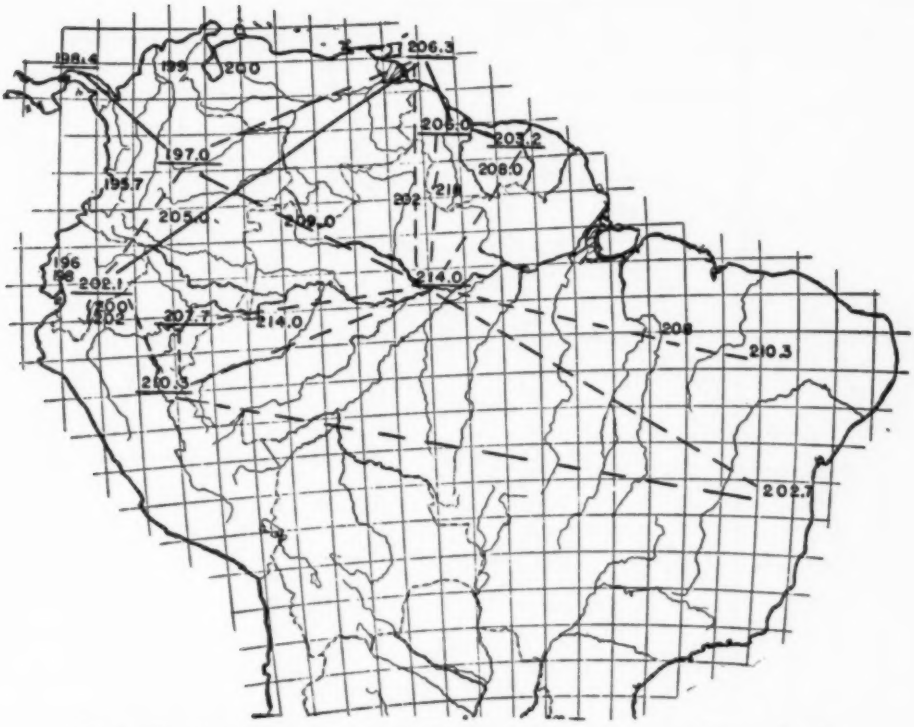

FIG. 5. GEOGRAPHICAL VARIATION IN THE NUMBER OF BODY ANNULI OF THE LEGLESS LIZARD *AMPHISBAENA FULIGINOSA*

Decimal numbers represent the number of annuli averaged for a sample from the place indicated. Numbers underlined are the nine major samples; others are smaller samples of 3 or 4 individuals each; integers represent single specimens. Numbers connected by solid lines do not differ by a statistically significant amount; broken lines indicate a statistically significant difference between the numbers they connect. (After Vanzolini, 1951.)

the coastal strip of the Gulf of Mexico wherever the latter is common.

At about the time of World War I, a third species of the same group became established at the Gulf port of Mobile, Alabama. This ant was identified with the dark Argentinian population of *S. saevissima*, the predominant species of the group from the Guianas south onto the Pampas.

> For about ten years [the Mobile population] remained both genetically homogeneous, corresponding to the dark southern race *richteri* Forel of the South American parental population, and relatively unsuccessful in its new surroundings. In the period following 1930 a smaller reddish form rose to abundance, interbred extensively with the original dark form, and apparently precipitated the species' explosive increase to pest proportions. By 1949 the reddish form had largely replaced the dark form, which had become limited principally to the southern strip of the main population and part of its eastern and western periphery and to two outlying, isolated populations in Mississippi. (Summary by Wilson, 1953).

Wilson found that over its native South American range, the yellow "typical" *saevissima* population of northern and central Brazil, gives way to the Argentinian black form through a broad clinal zone including Bolivia, the Chaco, and southeastern Brazil. The post-1930 reddish form of the Mobile area matched samples from the South American intermediate populations, and may well have arisen as a second introduction from southern Brazil or northern Argentina.

The map (Fig. 6) shows Wilson's plot of the growth of the main North American area of infestation through 1949; several smaller centers had

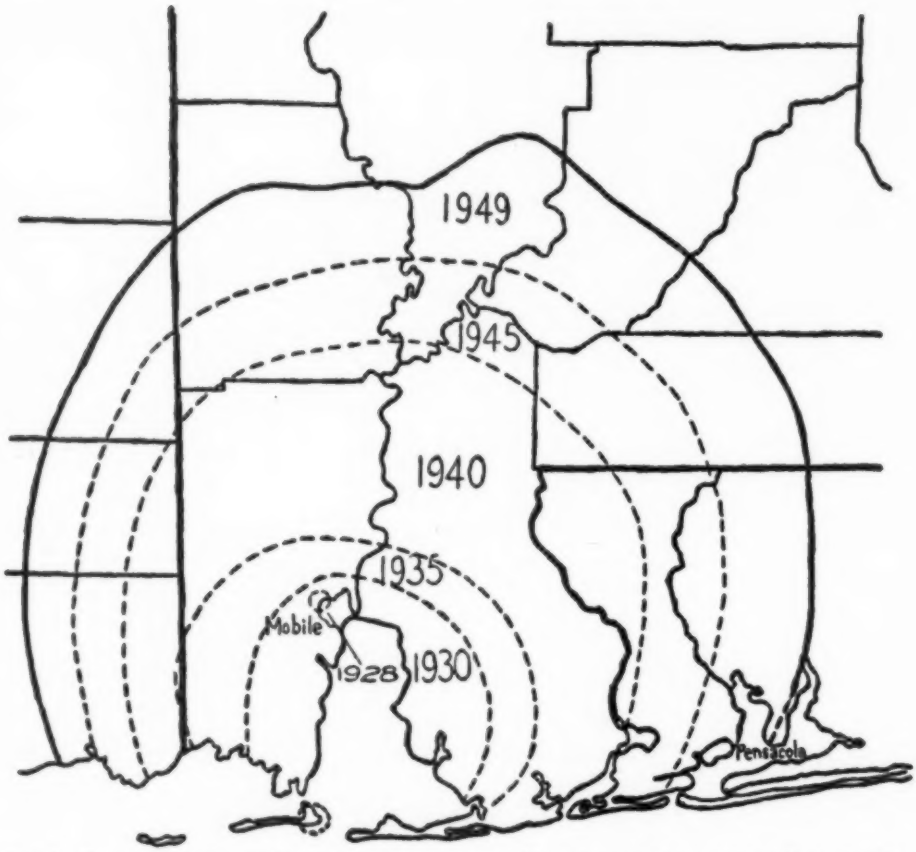

FIG. 6. ESTIMATED RATE AND DIRECTION OF SPREAD OF THE MAIN AREA OF SPREAD OF THE IMPORTED FIRE ANT, *SOLENOPSIS SAEVISSIMA*, IN THE CENTRAL GULF COAST REGION OF THE UNITED STATES, AS OF 1949

There were a number of smaller infested loci outside the main area in 1949, and many of these have since been engulfed by the spreading main area, according to recent surveys. (After Wilson, 1951.)

by that time become established a little farther north and west outside the main area, apparently most of them started accidently after transport by human commerce. Since 1949, the U. S. Department of Agriculture (Culpepper, 1953) has reported a considerable spread of the infested area, but the present proportions of light and dark phases remain unrecorded, except for a limited coastal area south of Mobile. Here in 1956 Wilson (pers. commun.) found during a brief survey that the frequency of dark-phase nests appeared to be lower than in 1949. Particularly did it seem to him that young dark-phase nests were scarce or absent in this region, so it may be that in their incipient stages, the dark-phase colonies are vulnerable to competition or aggression by the red phase.

The dark-phase colonies apparently are now limited to certain separated peripheral areas of the range and a few minor enclaves within the main area of infestation, and even where they occur, they are often in the minority (Fig. 7). All degrees of intergration link dark and red phases. As the red forms press outward, the dark forms apparently suffer both genetic swamping and competition-aggression, and consequently tend to extinction in most habitats. In spite of these forces at work against it, the dark form persists, genetically embedded, so to speak, in the dense and

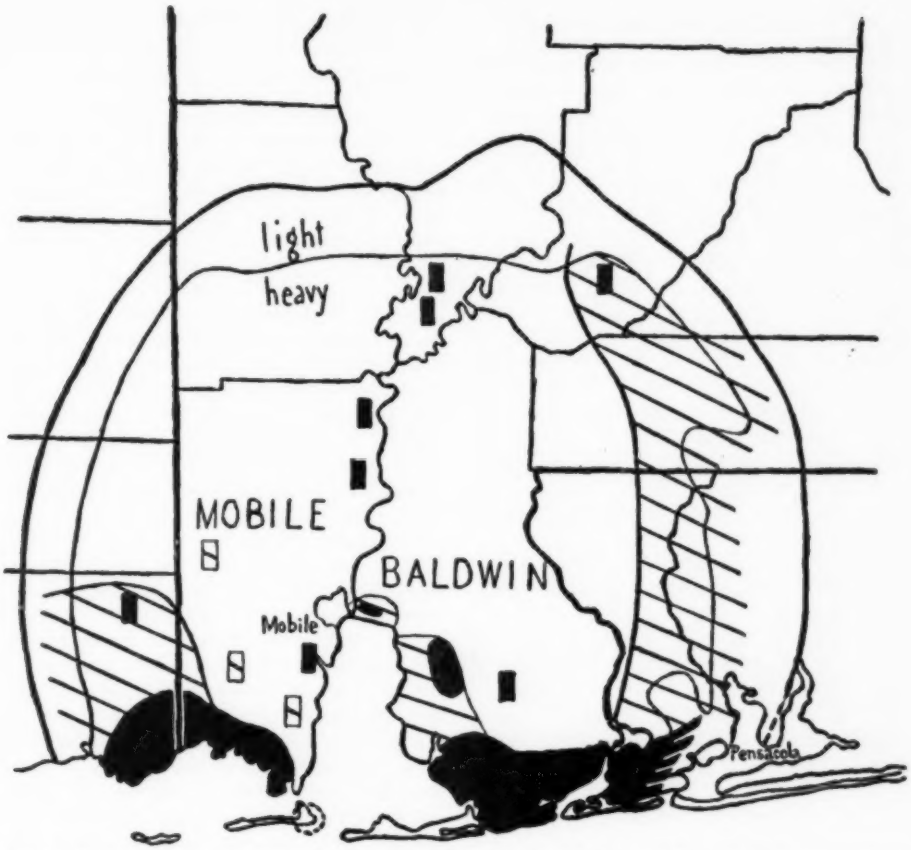

FIG. 7. DISTRIBUTION OF THE COLOR PHASES OF THE IMPORTED FIRE ANT IN THE MAIN AREA OF INFESTATION, AS OF 1949

Solid black represents areas with incidence of dark and intermediate phases of greater than 20 per cent; hatching represents areas with incidence of these phases of 5–20 per cent. Small black rectangles represent minor isolated dark-phase populations. In the centers of infestation outside the area shown in 1949, some populations were dark, others light; the present status of these is unknown. (After Wilson, 1951.)

expanding matrix of red populations. This case is very instructive in showing how, regardless of its origin in this particular case, a genetic change actually spreads from a central point of introduction and tends in this way to cause a central-peripheral differential.

It is also interesting to note that *S. saevissima* occupies a large, favorable central range with respect to *S. geminata* and *S. xyloni* in the New World. In the area of infestation in North America, *S. saevissima* has almost completely replaced its two congeners in areas where one or both were formerly abundant.

A perhaps even more remarkable case of centrifugal waves of change passing through a species range is that claimed for the land snail *Partula vexillum* Pease on Moorea in the Society Islands. Crampton (1932) believed that the evidence shows this snail to have alternated between dextral and sinistral types at least once, and perhaps twice, during a half century. He showed that the changes probably have taken place in centrifugal waves from a common center in the southern part of the island. This snail will bear watching in years to come.

Color Variation in the Common Hornet

Professor J. C. Bequaert has shown me the interesting color variation in the common Eurasian hornet (*Vespa crabro* Linnaeus). On the European Continent and eastward through Asia Minor and Siberia, the hornets are dark in color ("vars. *crabro, germana,*" etc.), with brownish or dull russet occiput and with the brown part of the second gastric tergum usually unrelievedly dark. In England, and then again in eastern Asia, in a broad zone extending from Manchuria and Korea south into Thailand, the color of the occiput is a clear yellowish, and many of the specimens show a broad yellowish-brown fascia within the brown part of the second gastric tergum.

The occipital color is not perfectly concordant in geographical distribution with that of the gaster, but yellowness on head and gaster tends to be more common in the British and the southern and eastern peripheral parts of the species range (Bequaert, 1931).

It is interesting to note that this hornet has been introduced into eastern North America, where it is now rapidly spreading. The immigrant populations are dark in color, corresponding to the central European population ("var. *germana*"). The Japanese hornets are darker in general than those from the Chinese and Korean mainland; Japan apparently is influenced chiefly from eastern Siberia, lying directly to the north.

Butterflies and Moths

In the New World tropical ithomiine butterflies of the *Melinaea lilis* complex, Forbes (1927) finds that "advanced" variants are more centrally located, while peripheral forms at opposite distributional extremes may closely resemble each other. He thinks that this situation "may be due to a more advanced form taking possession of the center of distribution, and driving the earlier types to the margins."

As dealt with by Forbes (1927, and pers. commun.) the *Melinaea lilis* complex consists of several named forms, distributed roughly as follows, from north to south:

imitator Bates	S. Mexico, northern Central America
scylax Salvin	Costa Rica
parallelis Butler	Panama
messatis Hewitson	Colombia
lilis Doubleday and Hewitson	Venezuela
dodona Hopffer	Peru, etc.

Of these, *scylax* may possibly be a species distinct from *lilis*, but this is uncertain. The geographical forms *parallelis* and *messatis* are hardly separable from each other, and feature a large black apical section of the forewing with usually three rows of small white spots. The dark longitudinal stripes of both wings are largely restricted to the apical portions. The *parallelis-messatis* condition grades into *lilis* in Colombia-Venezuela; *lilis* has a smaller black apical section of the forewing enclosing two rows of yellow streaks or elongate spots, and in addition, each wing bears two longitudinal dark stripes reaching to near the wing base on the orange field. The northern population (*imitator*) is almost precisely identical to Venezuelan *lilis*.

[In the clines *messatis-lilis-dodona*, these diagnostic characters of the "races" change one at a time, and not in geographical concordance. Fox (1955) intimates that his studies in the Ithomiinae have failed to reveal discordant geographic variation in this group, although he cites no examples. It is therefore of interest that Professor Forbes, long a student of the ithomiines, has been able to furnish evidence of discordance in *M. lilis* purely as a chance incident to the present study.]

Other possible cases among the Lepidoptera occur in *Papilio thoas*, in the migratory *Vanessa*, and in the moth *Eacles imperialis*.

The Marsh Fritillary (*Euphydryas aurinia*) of the British Isles has a peripheral form (*praeclara*) in Ireland, and transitional types are found in the western isles of Scotland. It is this butterfly upon which Ford and Ford (summary in E. B. Ford, 1945) made their now widely appreciated observations on population fluctuation and variation. A record of an isolated English colony of *E. aurinia* was kept back to 1881, and high density peaks occurred during 1894–1897 and 1925 to beyond 1935. The later peak was reached by a rapid increase in numbers after a long period of scarcity. During this increase period, the variation widened explosively to produce all sorts of extreme variants, including some deformed individuals. After the rapid increase stopped, extreme variants disappeared and the colony settled down to a more homogeneous type. This type, however, differed somewhat from the one prevailing during the earlier population peak.

Observations of this sort are regrettably rare, considering their interest and importance, but now population genetics is inevitably entering a period of detailed investigation of density-reactive variation (see discussion of *Drosophila pseudoobscura* group below). We especially need information on the variation of strongly emigratory animals as correlated through time with density peaks and troughs.

Adaptive Inversions in Drosophila

Drosophila of the *willistoni* group are among the wild fruit-fly predominants in tropical America. America. *D. willistoni* itself is a very common and widespread species, ranging from Florida and central Mexico southward to Argentina. Some 40 identifiable chromosomal inversions have been found in *D. willistoni*, and their frequency at any given locality has been linked to the probable number of ecological niches exploited at that place by this species. Thus, the number of inversions is highest in central Brazil, in regions where luxuriant rainforest and savannah interdigitate, and where *D. willistoni* far predominates in numbers over its three sibling species (*D. paulistorum*, *D. tropicalis*, *D. equinoxialis*). But the numbers of inversions present in *D. willistoni* fall off toward the northern (Central America) and southern (southeastern Brazil) extremities of the range, and drop drastically in local regions of eastern Brazil that are ecologically unfavorable for the species. The *D. willistoni* inversion counts are also lower in certain localities in the Amazon Basin that are ecologically favorable, but in which one or more of the three sibling species have reached a high frequency; this may be "character displacement" at the level of chromosome morphology (da Cunha, Burla, Dobzhansky, 1950).

These same authors indicate that the left limb of the X chromosome in *D. willistoni* may show peripheral similarities in its inversions.

> XL is the most "difficult" chromosome, owing chiefly to the prevalence of the geographically different gene arrangements. Crosses of the standard strain to strains from south Brazil usually give the quintuple inversion . . . (B, D, F, G, H), while the triple inversion (B, C, D) is observed in crosses of the standard to Central American (Costa Rica, Guatemala, Mexico) strains. The quintuple and the triple inversions have two elements (B and D) in common, which means that with respect to these two inversions the Central American and the South Brazilian strains are actually more similar than either of them is to the standard strain which is of geographically intermediate origin.

In breadth of range, in average overall abundance and dominance, and in numbers of inversions present, the four species of the *willistoni* subgroup have the relation *willistoni* > *paulistorum* > *tropicalis* > *equinoxialis*. For the most part, these species have appeared to possess concentric range boundaries centered on equatorial Brazil, with *D. equinoxialis* the most limited in extent and *D. willistoni* the broadest (Burla *et al.*, 1949; Dobzhansky, Burla, and da Cunha, 1950). This would appear to be the opposite kind of situation to the central-peripheral ones we have been discussing, and therefore not easy to explain unless we allow that such "niche-rich" areas as tropical Brazil may provide the best refugia of all due to mosaic discontinuities of their biota. But now Townsend (1954) has found populations in the Greater Antilles that he assigns to *D. tropicalis* (as a "subspecies *cubana*") and to *D. equinoxialis*, as well as to *D. willistoni*. It is clear that much remains to be learned concerning the distribution and taxonomy of the *willistoni* sibling species before we can understand exactly what the situation is here with respect to "relict" forms. If investigations continue over the years, it may be possible to chart some interesting evolutionary changes in this complex. More attention should be paid to *D. nebulosa*, a *willistoni* group member that tends to have a peripheral distribution and is more xerophilic than *D. willistoni*, so that the ecological and geographical distributions of the two are roughly complementary.

North American Camel-crickets

Hubbell (1936, 1954, 1956) calls attention to two most interesting "centripetal clines" in characters of two North American species of the orthopteran genus *Ceuthophilus*. The case of *C. uhleri* Scudder is described in detail:

> This wingless camel-cricket is a species of the eastern deciduous forest region, ranging from Iowa and Kansas east to southern New York and coastal Virginia, and south in a narrowing wedge to the Gulf Coast in Alabama and Florida. It shows a centripetal pattern of clinal variation in two characters of the genitalia [Fig. 8], one of the sternum, and one affecting the proportions of the legs and their spinous armature. Populations in-

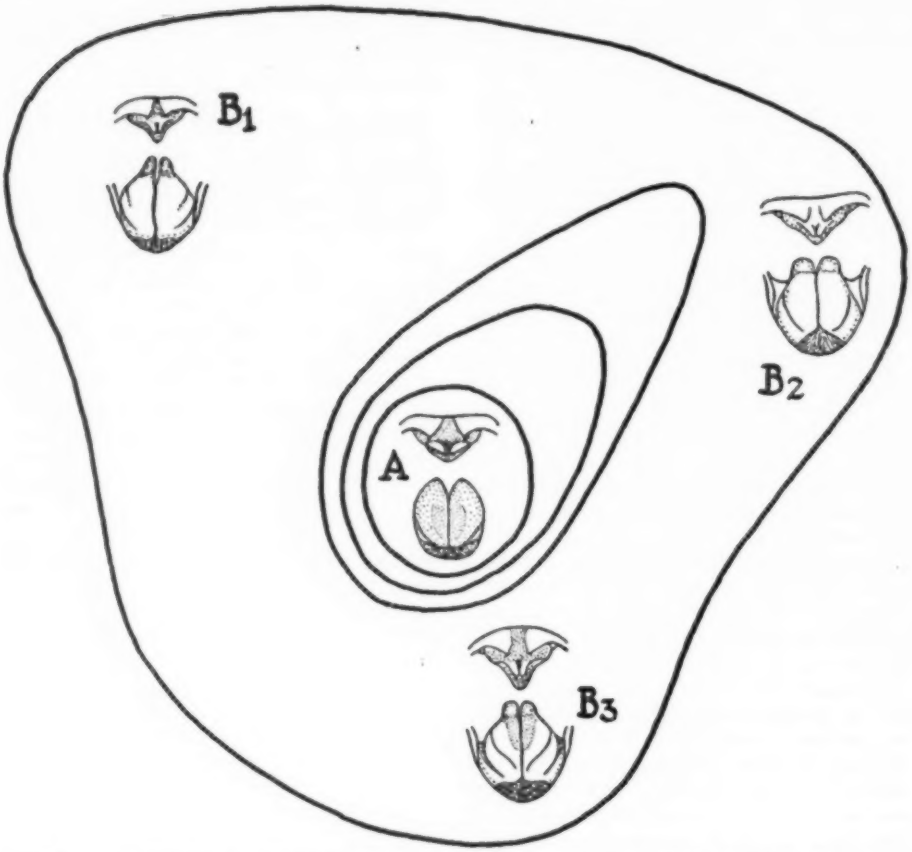

FIG. 8. GEOGRAPHICAL VARIATION OF TWO GENITALIC CHARACTERS IN THE NORTH AMERICAN CAMEL CRICKET, *CEUTHOPHILUS UHLERI*

Population A, in north-central Alabama, has the apices of the epiproct (upper figure) and subgenital plate (lower figure) unconstricted and the marginal thickenings of the former separate and divaricate. In peripheral population B the apices of these structures are constricted and the marginal thickenings of the epiproct are approximated and subparallel distad. B_1 (Indiana), B_2 (Maryland), and B_3 (west Florida) differ in size and robustness, but are much more like each other than any of them is like population A. Isophenes may be drawn between the center and periphery of the range approximately as shown, the axis of elongation being along the Appalachian Mountains. (After Hubbell, 1954.)

habiting Indiana, Maryland, and Florida are more similar in respect to these features than any of them is to the central population in northern Alabama. The isovariant lines or isophenes form contours centering on northern Alabama and running out along the Appalachian axis. Superimposed on this cline of covariant characters is another, a north to south increase in size, which tends to obscure the resemblances of the peripheral populations. . . . An attempt to apply conventional nomenclature to this situation would have resulted in a peripheral subspecies extending from Florida to Iowa to New York in a ring around a central subspecies, which seems absurd.

African Squirrels

If only as a warning against too facile an interpretation of central-peripheral variation, we should perhaps include an example that can be handily explained on purely ecological grounds, just as well as along the lines we have been exploring.

The squirrels of the genus *Heliosciurus* have

been referred to as many as 45 subspecies distributed among a maximum of 11 species. Ingoldby (1927) considers that all of these populations constitute a single species inhabiting Equatorial Africa, but one varying strongly in size and especially in color over this wide area. The variation assumes a somewhat concentric pattern centered in the Congo rainforest, and remote samples from around the savannah periphery often resemble each other much more closely than they do the central forest strains. There is complete intergradation from the rainforest areas through lighter woodland and savannah to grassland types. In this case, the central-peripheral pattern may be due entirely or chiefly, as Ingoldby suggests, to close local adaptation following the vegetation types, which also run somewhat concentrically around the Congo. This squirrel is a promising subject for further and more detailed study.

In the examples cited above, the emphasis has rested on variation known or thought to be confined to single species. In each case, some theoretical expectation of central-peripheral differentiation appears to have been fulfilled. In a few cases, perhaps, the differentiation can be correlated more or less closely with concentric vegetational or other ecological zones (*Heliosciurus*), but certainly the other examples cannot all be easily linked to environmental gradients. Central-peripheral variation has been repeatedly discussed before, the apparent lack of environmental correlation duly noted, and the cause even laid to "*Alleldiminution*" through "*Elimination*" (Reinig, 1939), or to "the instability of certain genes and the loss of alleles in the border populations of an expanding species" (Mayr, 1942, p. 96). Such interpretations seem to come under the general "distance effect" or "geocline" concept sometimes discussed in taxonomic papers. Mayr, however, believes that in these cases "selective factors are involved to some extent."

Various ideas and data more or less closely related to the present hypothesis are apparently widespread in the literature (e.g. Matthew, 1915; Lutz, 1916, Timoféeff-Ressovsky, 1940, among others), and it would be interesting but difficult to trace the historical continuity of thoughts along this line. For instance, there is the venerable notion that variation in the genus *Homo* has proceeded prevailingly outward from more central continental areas into peripheral Europe, riding on successive population waves. There seem to be no serious objections to this point of view. It may well be that speciation in early man depended on central-peripheral processes as outlined in the present hypothesis. In fact, I predict that good evidence for this will be available in a very short time.

With the phases of contraction, populations of the species disappear from the peripheral areas, except in relatively restricted refugial pockets or islands that are favorable enough to allow survival of some expansion-phase remnants. At this stage, or course, the central populations are geographically isolated from the peripheral remnants, so as to permit the expected accumulation of genetic differences between them.

I do not think this point requires much documentation. Every taxonomist and field ecologist should be able to call up his own examples of range contraction, and of animal populations isolated from their main species range. We have already reviewed several relevant cases. Such populations may or may not show detectable differences from one another, but there can be little doubt that they do differ genetically in some ways, even if only in the frequencies of one or a few alleles.

When differences appear in peripherally isolated populations, they are often more or less obviously adaptive to the local environmental conditions. They can also represent visible side (pleiotropic) effects of cryptic adaptive characters, such as physiological or behavioral ones. Perhaps we must also consider random fixation and gene loss, but as studies of field populations accumulate, these processes seem ever less significant as forces in evolution.

Unfortunately, under the "subspecies method" of describing geographical variation, the local characters peculiar to isolated populations are usually emphasized, and broad interpopulation similarities are often neglected. In this way, major trends and patterns of variation are nearly always masked to some extent in taxonomic papers. And on one occasion, I was told by a competent herpetologist that he had spent much time analyzing the geographic variation of a common snake species, only to end by shelving the project and the data for the reason that "the races were not clear-cut enough to name!" For a fuller critique of the subspecies concept, see Wilson and Brown (1953).

In spite of the serious difficulty one encounters in attempting to extract relevant information from

a subspecies-oriented literature, we have seen in the last section that central-peripheral patterns of variation (centrifugal geoclines?) do occur widely, often cutting across the more obviously and simply adaptive clines (ecoclines) or local character-types (microraces). This central-peripheral differentiation exists in theory even for completely continuous populations (see Fig. 1), but it can be the basis for species separation only if geographical isolation intervenes to block gene flow (Mayr, 1942).

During the contracted phase, of course, even the central populations may become fragmented or patchy in distribution, as has been stressed repeatedly by Sewall Wright and other authors. This is especially true in very favorable areas, such as tropical rain forest, where "mosaic" distributions tend to be determined more by biotic than by physical environmental factors. Under such conditions, gene complexes presumably can develop "coadaptedness" and can come to prevail in particular demes, both central and peripheral. Interdeme competition and selection (Wright, 1956) can be expected to become increasingly effective after the populations enter the phase of density increase and expansion.

If, as must happen in only a small proportion of cases, the differences mount to the point of reproductive isolation, the next phase of expansion will establish the geographical contact needed to confirm the new species difference. The new, contiguous or overlapping species will likely be forced to avoid hybridization (through reinforcement of the reproductive barriers) and competition (through ecological or geographical displacement). The chances are that, in most such contacts, the "new central" species overwhelms the "old peripheral" species by competitive pressure, or, more likely, by means of adaptations of the general "aggressive" type, functioning to remove or incapacitate competitors. But if the two new species can specialize to divide the exploitable environment between them, they may both persist.

It seems likely that most expansions find reproductive isolation between central and peripheral elements not complete enough to prevent swamping when geographical contact is reestablished. The alternative possibility is that species arise very frequently, but that the peripheral ones are wiped out by competition or aggression at an almost equal rate. Probably not more than a fraction of the range fluctuations suffered by a species can produce successful, indefinitely self-maintaining daughter species. Otherwise, the number of animal species would be vastly greater than it is. We do know that centrifugal swamping exists, as in the case of the imported fire ant, but it does not seem possible at present to guess at the proportion of cryptic "trial species" that may survive for a few generations and then succumb, unnoticed by even the most eagle-eyed taxonomist or population geneticist. For an interesting "trial species" situation in the plant genus *Clarkia*, see H. Lewis (1953).

But in at least a small proportion of contacts, there will exist differences of the sort that add up to reproductive isolation between relatively successful populations. In such cases, reinforcement of the isolating mechanisms will normally develop. To the extent that all or some of the same differences tend to be preadaptive for different niches, the two populations will diverge further along these same lines in order to minimize competition between them. These two processes add up to character displacement, a subject reviewed in detail by Brown and Wilson (1956).

Character displacement means that differences between closely related species will normally tend to be greater where they occur together (sympatrically) than in populations of either occurring apart from the other. We should expect to find character displacement arranged on a central-peripheral basis, and indeed such examples appear to exist in the crossbill and the *Drosophila pseudoobscura* subgroup, discussed below.

Ecological displacement may of course tend to lead to differences in spatial distribution, or geographical displacement. In some cases also, geographical displacement will occur when two newly reproductively isolated species have so nearly identical ecological requirements that their ranges can meet without either species being able to penetrate significantly into the area of the other (summary of cases in birds by Vaurie, 1955).

In accordance with the concept of geographical displacement and the expected higher evolutionary potency of centrally evolved species, we should expect to find the central-peripheral pattern extending to pairs of closely related species. This pattern will be obvious at first only in those cases where range expansion is free to develop in all, or at least in several, compass directions. We must look for such cases in the reported "fringing" and widely discontinuous species ranges, of which a few are examined below.

The Crossbills

Were I an ornithologist, I think that the finches of the genus *Loxia* would take up most of my research time. No group of birds seems to offer more tantalizing problems in that area of biology where systematics, ecology, zoogeography, population dynamics, and ethology overlap.

The density-reactive irruptions of the crossbills have already been discussed. It may now be useful to mention some features of the taxonomy and distribution of these birds. Of the three main types, *L. pytyopsittacus* has a very deep, parrot-like bill (Fig. 9A) and is restricted as a breeder to countries around the eastern Baltic Sea. Apparently its thick bill is correlated with its preference for the seeds of pines as a diet.

The white-winged or two-barred crossbill, *L. leucoptera*, breeds from northern Scandinavia eastward through boreal Eurasia and the northernmost American forests. In Europe, at least, it is said to prefer the seeds of larch, and its bill is generally weaker than in the other kinds of crossbills of the same or nearby areas. In the mountains of Haiti and the Dominican Republic there are isolated populations of crossbills (*L. megaplaga*) very similar to *L. leucoptera*, to which they are customarily attached as a race. These probably feed chiefly on pines, the mountain conifers of Hispaniola, and the bill is correspondingly thicker than in the nearctic *L. leucoptera*.

The dozen or more named populations usually considered collectively as *L. curvirostra*, the "red crossbills," breed very widely in the coniferous forests of Holarctica, especially in those regions not or thinly populated by *L. leucoptera*. Many populations of *L. curvirostra* have medium bills (Fig. 9C) and tend to feed mainly on spruce, fir, and pine, their preference varying in different populations. Others have deep bills (Fig. 9B) intermediate between those of "typical" *L. curvirostra* and *L. pytyopsittacus*: *L. anglica* (=*scotica*) breeds in Scotland, *L. balearica* in the Balearic Islands, *L. poliogyna* in North Africa, *L. guillemardi* in Cyprus, *L. estiae* on Oesel Island in the Baltic, off Estonia, and there is a similar type in the Crimea. The chief food of these intermediate-thick-billed forms is known or presumed to be pine seeds. It should be noted that these intermediate bill types are situated peripherally to the main European crossbill populations. Griscom considered that the intermediates signified conspecificity for *L. curvirostra* and the thick-billed

FIG. 9. CHARACTER DISPLACEMENT IN BILL FORM IN EURASIAN CROSSBILLS, GENUS LOXIA

A, *L. pytyopsittacus* from Uppsala, Sweden. B, *L. pytyopsittacus* or *curvirostra*: intermediate form from Scotland. C, *L. curvirostra*, "typical" form, from Bashkiria, Ural Mts. (Adapted from Kirikov, 1940.)

forms, including *L. pytyopsittacus*, but all of these intermediates can now be considered either as distinct species or as undisplaced peripheral populations of either *L. curvirostra* or *L. pytyopsittacus* when viewed in the light of the character displacement theory (Brown and Wilson, 1956). Especially is this so when we recall that L. *curvirostra* and *L. pytyopsittacus* breed, apparently without intergrading, in the same general areas.

The pattern of geographical variation in the crossbills, at least in the absence of more detailed analysis of particular characters, seems to be roughly one of zones of differing bill depth alternating from the center in northern Europe outward. The North American red and white-winged crossbills both average smaller in body size and have smaller bills than their European counterparts, but size and bill depth recover to nearly or quite the status of European *L. curvirostra* in the Mexican populations of this same species. A similar situation exists in southeastern Asia, terminating in the Annamite population. Such alternation has already been mentioned above in the variation of the drongo *Dicrurus leucophaeus*. It may even often be true that waves of characters proceeding outward from the center tend to contrast, each with its predecessor, perhaps as a result of varying degrees of character displacement. These cases need close study before we can say much more about the nature, let alone the causes, of central-peripheral *character alternation*.

Divergent extralimital red crossbills inhabit the Himalayan region, southern Annam, northern Luzon, and Newfoundland; the last two populations (*luzoniensis* and *pusilla*) may well be distinct species. With the British and isolated Mediterranean resident strains, these peripheral populations indicate that emigrants can and occasionally do permanently establish themselves far beyond

the normal breeding range. We know that crossbill populations frequently disappear from peripheral areas where they have bred and increased for a number of successive years. Apparently this is true of the crossbills that flourished and spread in Ireland after the irruption of 1887, and it may apply also to populations in the southern Appalachians, parts of Spain, and elsewhere.

We need much more information on the crossbills. Especially required are observations on the pairing specificity and behavior in areas and at times when two or more morphological types are breeding together; these could possiby be supplemented by laboratory breeding experiments. Also needed is a more complete and detailed comparative account of feeding habits for all the recognizable populations, linked with a new quantitative study of bill size and shape as independent variates for all the crossbills.

But even with the incomplete evidence we have at the moment, the crossbills seem to provide nearly all the features one might expect of a widespread and actively evolving species group or species-succession of the centrifugal type (data chiefly from Griscom, 1937; Kirikov, 1940; Lack, 1944).

Sibling Species in Drosophila

In western and southwestern North America occurs the much-studied *pseudoobscura* subgroup of the *Drosophila obscura* group. This subgoup includes four extremely close species: *D. pseudoobscura*, *D. persimilis*, *D. miranda*, and *D. frolovae*. *D. frolovae* is recorded only from the type locality in Michoacan, Mexico, and practically nothing is known about it. *D. miranda* is a rare species restricted to the Pacific Coast area (see map, Fig. 10). *D. persimilis* is more common and has a wider range, but is also a Pacific region endemic. *D. pseudoobscura* is widespread in Mexico and western North America, blanketing the ranges of *D. miranda* and *D. persimilis*, except that *D. persimilis* extends a little farther north and west in British Columbia and reaches higher elevations in the mountains where both species occur in the same general region.

D. pseudoobscura and *D. persimilis* overlap broadly in local distribution and ecological preference, and the two species commonly breed side by side in the same sap fluxes, so that some competition is apparently inevitable. Their relative abundance fluctuates seasonally and over the years, but *D. pseudoobscura* seems generally to predominate.

D. miranda has a third chromosome arrangement very like the Hypothetical primitive type, whereas in *D. pseudoobscura* and *D. persimilis*, the homologous third chromosome is highly polymorphic in arrangement (Dobzhansky and Epling, 1944, summary in Patterson and Stone, 1952, pp. 18–20, 53–54, 191–199, figs. 35, 55–58).

Although from morphological evidence it seems that the *pseudoobscura* subgroup is most closely related to some Palearctic members of the *obscura* group, one might judge that the subgroup has been in the New World for a long time. Certainly it has undergone and is now undergoing active evolution in western North America. In my opinion, its present main center of evolution probably lies in the southwestern United States and northern Mexico. *D. pseudoobscura* occupies this center and areas peripheral to it. The Pacific Coast States constitute a strip of favorable territory, but one that is smaller and probably to be considered peripheral, on the whole.

The country lying between the Sierra Nevada of California and the Rockies is for the most part relatively unfavorable for occupancy by the *D. pseudoobscura* subgroup, and *D. pseudoobscura* populations living here lack some inversions found on either side. It seems likely that this general region marks more or less precisely the previous gap that must have separated the incipient *D. pseudoobscura* stock from the *D. persimilis* stock for long enough to allow reproductive isolation to develop between the two. It is *D. pseudoobscura* that has subsequently been able to cross the gap, doubtless on the crest of more than one "population-wave."

To me, the *pseudoobscura* subgroup looks like a fairly typical central-peripheral situation involving at least three "species-waves" as represented in the order *miranda*, *persimilis*, *pseudoobscura*. In addition to the general distributional pattern of the three species (and perhaps also *D. frolovae*), we have other scraps of possible evidence mentioned in passing by Dobzhansky and Epling (1944).

First, it has been found that sexual isolation is stronger between *D. miranda* and *D. persimilis* than between *D. miranda* and *D. pseudoobscura*, suggesting that the former pair have been sympatric for a longer time. Second, the abundance of *D. pseudoobscura* increases in general as one goes from the Pacific Northwest toward the east and south. This

FIG. 10. MAP SHOWING THE RANGES OF THE FOUR SPECIES OF DROSOPHILA OF THE *D. PSEUDOOBSCURA* SUBGROUP IN WESTERN NORTH AMERICA AND GUATEMALA

The approximate limits of the range of *D. pseudoobscura* are indicated by the heavy lines. The approximate range of *D. persimilis* is indicated by solid black (individual locality records as of 1944 are round white dots). Locality records for *D. miranda* are marked by small crosses, and the sole locality for *D. frolovae* by an encircled letter "f." (From Dobzhansky and Epling, 1944, and other sources.)

may be correlated in part with temperature and moisture gradients, as suggested by Dobzhansky and Epling. Third, there exists a certain type of Y chromosome ("type I") that occurs

> . . . in most populations of *persimilis* and also in certain populations of *D. pseudoobscura*. Judged superficially, this fact might be taken as evidence of introgression. This chromosome type, however, has never been found in the populations of *D. pseudoobscura* from California, Oregon and Washington, where it would be expected because of the presence of *D. persimilis*, but only in populations found in southern Arizona, Mexico, and Guatemala, far removed from the range of that species. The type of Y chromosome is similar in appearance in the two species, but it is not impossible that in reality the chromosomes in question are different. If they are in fact genetically identical, any hybridization must have taken place in the remote past.

This Y chromosome situation seems to qualify as a further case of character displacement, comparable to the example already given of the bill depth in crossbills. It would be interesting to know what, if any, adaptive correlations this chromosome character has.

Dobzhansky (1956) has reviewed and added to the data available concerning fluctuations in the frequency of third chromosome inversions in *D. pseudoobscura* and *D. persimilis* in California. These gene arrangements show fairly regular seasonal shifts in relative frequency of occurrence, so that a given one may predominate during a given month in most years. There are also longer-term rises, falls, and repetitive fluctuations in frequency of individual arrangements. It now begins to appear that at least some of the frequency shifts in third chromosome polymorphs are reactive to density changes in the fly populations, especially in view of the recent findings of Birch (as cited by Dobzhansky) relative to the Standard and Chiricahua inversions.

Since 1945, an inversion known as Pike's Peak (PP) has become increasingly common in *D. pseudoobscura* populations of California. Before that date, PP was known only as a rarity in central California, and was not found in California localities where it later became frequent. Previously, PP had been more common in the Rockies, in Texas, and in northern Mexico. Dobzhansky thinks it unlikely that the California rise is due to the "introduction of PP chromosomes into California from elsewhere," but the basis for this belief is not clear to me.

There seems to be no outstanding reason why PP or any other inversion should not be expected to increase its area of occurrence, granting that it is adaptively positive. Surely, it must have spread at some time, even if not initially during the years immediately before and after 1945. It is also possible, of course, that PP has arisen to prominence in California because some of the genetic material it presumably holds together has changed in an adaptively positive way. Such a change would still have a geographic origin and would tend to increase its geographical range.

To my way of thinking, at any rate, there exists the possibility that either PP or some potent constituent now associated with this inversion is currently spreading from (perhaps) a Texan or Mexican area of origin. Considering the opportunities open for long-distance transport of *Drosophila* propagules (Dobzhansky and Epling, 1944), the observed (probable) rate of spread is unremarkable. It would be interesting to study dispersal, emigration, and colonization of *D. pseudoobscura* under differing population densities in nature.

There is some direct evidence to indicate that dispersal is density-reactive in this species and in *D. persimilis*. Carson (1951) found in California that adults of these species, when visiting their favored natural feeding and oviposition sites at slime fluxes on the trunks of *Quercus kelloggii*, tended to avoid fluxes already containing older larvae or pupae of *Drosophila*.

Fringing Forms in European Bumblebees

"*Fringing distribution*" is a term proposed by O. W. Richards (1935) and applied to the populations themselves as *Randformen* by Zimmermann (1950). Richards studied the European distribution of two very closely related species of bumblebees of the *Bombus agrorum* group. *B. muscorum* ranges in Europe from Rumania, Turkey, Italy, and Spain northward to the Baltic, and through England, Scotland, and Ireland. *B. smithianus* occurs on certain of the islands fringing the coasts of England, Scotland, and Ireland, in particular those where *B. muscorum* is absent. The two species have been taken at Ross in western Scotland, but they seem here to be elevationally separated. The Hebrides, Shetlands, Faroes, Norway, and Finland have *B. smithianus*, which continues around through the Archangel district and southward into Russia for an undetermined distance. Richards compares

this distribution with that of some microtine rodents of Europe (discussed below) and favors the explanation that *B. smithianus* is being overtaken by the more centrally-placed *B. muscorum*, which is able to replace *B. smithianus* when it meets it. Richards suggests that the chief point of competition could be for nesting sites, usually old nests of voles. He also indicates that *B. muscorum* itself may be under increasing pressure from other common and centrally-placed members of the same (*agrorum*) species group, since *B. muscorum* tends to be abundant only when occurring apart from these.

New World Butterflies of Genus Euptoieta

The fritillaries of the genus *Euptoieta* range from temperate North America to southern South America. There are two close but distinct superspecies, *E. claudia* and *E. hegesia*.

E. claudia is resident in the United States and in Mexico, Guatemala, and Jamaica at higher elevations. A very similar form, *hortensia*, is usually placed as a race of *E. claudia*; this form is found in Bolivia, the La Plata Basin, and neighboring mild regions. Other *claudia*-like populations occur in upland Ecuador, Colombia, Panama, and Costa Rica, and these are generally held to represent another very close species, *E. bogotana*, in superspecies *claudia*.

E. hegesia ranges from the southern extremities of the United States southward through the West Indies, Mexico, and tropical South America, mostly at lower elevations. Where it meets the range of *E. claudia*, as in Mexico, Jamaica, Guatemala, and at the northern and southern borders of its range, *E. hegesia* shows only slight distributional or altitudinal overlap with *E. claudia*.

The two superspecies feed as larvae on the same general food plants, mainly of the Passifloraceae and Violaceae. There is little doubt of their close relationship, and it would be interesting to know whether the ranges of either or both species are expanding or contracting.

Neotropical Dacetine Ants

The distribution of the small but common ant *Strumigenys louisianae* closely resembles that of the *Euptoieta claudia* superspecies, except that it is more widespread in the Greater Antilles. *S. louisianae* is replaced by a very similar species, *S. unidentata* Mayr, in Amazonas and central Brazil, and the two overlap, so far as known, in southeastern Brazil.

Melanesian Ants of Genus Anochetus

E. O. Wilson has called to my attention the distribution of ants of the *Anochetus cato* group in New Guinea and surrounding archipelagoes. Diagnostic characters, variation, and synonymy of the *cato* group are outlined in a manuscript to be published eventually by Wilson. New Guinea proper, the Bismarck Archipelago, and the Solomon Islands as far as San Cristobal are inhabited by *A. cato* Forel, apparently a single species that varies strikingly in color from one part of its range to the next (i.e., is "polytypic"). Closely related to *cato*, but differing by a clearcut sculptural character, are four populations comprising "superspecies *isolatus*." These are: *isolatus* Mann (Santa Cruz Islands, and relatively rare on Malapaina Island in the Three Sisters Group, near San Cristobal, where it coexists with *cato*); *splendidulus* Yasumatsu (Truk); *seminiger* Donisthorpe (Waigeo Island, off the Vogelkop), and *splendens* Karawajew (Aru). Aside from color and perhaps one or two other slight differences, these four peripheral forms are very close, and it is entirely possible, in view of the uncertainty principle, that some or all of them are still conspecific, instead of being superspecies members. Wilson has retained the four as species only by arbitrary designation.

While undoubtedly there remain unsampled many populations of both *A. cato* and the *A. isolatus* superspecies, the pattern as seen from the present material is certainly suggestive of a central origin and centrifugal spread of *A. cato* at the expense of the *isolatus* type.

Another similar case among Melanesian ants involves *Strumigenys szalayi* Emery (New Guinea) and the very similar *S. australis* Forel (northern Queensland, Micronesia, Philippines).

Palearctic Wagtails

The birds of the yellow wagtail complex have been studied by Williamson (1955), who recognizes two species, *Motacilla lutea*, representing the greenish- or yellow-headed populations, and *M. flava*, for the populations in which the head is more or less blackish, gray or bluish. (But see Mayr, 1956).

M. lutea breeds in three separate areas: (1) Britain and isolated pockets on the Atlantic

coasts of France, Holland, Heligoland, and Norway; (2) the Kirghiz Steppes, from the Volga River, and the Caspian and Aral Seas eastward to the headwaters of the Yenesei River; (3) Lena River eastward to Sakhalin and the Kurile Islands. These areas are on or close to certain boundaries of the distribution of *M. flava*, which has a much more extensive range in northern Eurasia (extending even to Alaska in the east) and is widespread in the Mediterranean area. Williamson agrees with Johansen, an earlier reviser, in

> . . . regarding the yellow-headed populations as the most primitive, and the dark- and blue-headed forms as derivatives of interglacial and postglacial origin whose subsequent spread has confined the yellow-headed birds to somewhat restricted ranges.

Microtine Rodents of Europe

Zimmermann (1950) discusses the *Randformen* of the rodents *Clethrionomys glareolus*, *Microtis agrestis*, *M. arvalis*, *M. oeconomus*, and *Arvicola amphibius* in Europe. In each of these cases, the central European population tends to be smaller in size. The peripheral populations on small offshore islands or in Britain, the Iberian Peninsula, and Scandinavia are larger and tend to be alike in size despite the considerable climatic differences occurring over the fringes of Europe where they occur.

The bank vole, *Clethrionomys* (=*Evotomys*) *glareolus*, has interested several authors (Hinton, 1926; Zimmermann, 1950; Steven, 1953) because of its peculiar distribution and variation. This superspecies is distributed over much of temperate and boreal Holarctica (as *rutilis*, *gapperi*, etc., in North America). In Europe there exist, roughly speaking, two extreme forms. *Glareolus* is smaller, usually has the reduced *simple* type of upper third molar, and is frequently lighter in color; it is the common lowland form over most of the continent and (as the scarcely differentiated "race *brittanicus*") on the mainland of England and Scotland. Larger forms, which for convenience can be grouped under the name *nageri*, have predominantly the *complex* type of upper third molar, are often rather dark in color, and are distributed chiefly in peripheral islands and, on the continent, in high mountains. Various degrees of morphological intergrades are known from place to place.

Large size seems to be the most consistently peripheral of these characters; tooth type is less regularly so, and dark coat color is only rather erratically associated with the periphery of the range.

It is puzzling that Hinton considered *glareolus* closest to the primitive type of the superspecies, when his evidence indicates, at least to me, that *nageri* or something like it may have been the earlier form. And when Hinton comes to speculate on the past movements of the forms, he has *nageri*-like waves moving outward first, to be overrun by later arrivals of the *glareolus* strain. He describes from Britain *nageri*-like Pleistocene fossils, and Post-Glacial remains that are most like the present *glareolus*, whereas present British mainland voles are all *glareolus* ("*britannicus*").

Zimmermann felt that the peripheral *nageri*-like populations were the survivors of an old, wide-ranging type in process of being replaced by a related strain from the center outward. He considered, however, that all of the forms concerned belonged to a single species.

Steven (1953) studied the British representatives of this complex. These include a widespread population of a smaller, lighter type ("*britannicus*") with predominantly simple upper third molars (very close to the "nominate race" of *glareolus* from the continent) inhabiting the British mainland and only a few close-in islands.

Three other disjunct minor populations occur on islands along the western fringe of Britain: Raasay and Mull in the Inner Hebrides, and Skomer farther south. These three populations all consist of voles significantly larger than the mainland ones; two of them (Mull and Raasay) are darker in color; and two of them (Skomer and Raasay) have a majority of upper third molars of the complex type. The color and molar characters appear to be unifactorial.

Steven made some crosses between these populations. The crosses Mull male × Skomer female and Skomer male × Raasay female "have so far been carried through more than a single generation, and show no sign of hybrid sterility, rather the reverse." This is interesting in view of the great distance along the British west coast separating Skomer from the Inner Hebrides.

Three other crosses, Skomer male × Mull female, Raasay male × Mull female, and Mull male × *britannicus* female, produced offspring, but further results awaited the maturity of these young at the time of his writing. Steven was unable to rear young from the Raasay male × *britannicus* female, an interesting result in view of the fact that these

two parent strains are the only ones that differ by all three characters: size, color, and third molar type. Steven thinks that

> ". . . the variety of hybrids already obtained, namely, half the total number of combinations possible, makes it unlikely that speciation has proceeded as far as a sterility barrier in any case, though there may be a partial one between the island and mainland stocks, since these crosses have been much more difficult to make than inter-island ones. We are not yet in a position to say why this should be so or to express it quantitatively. It may simply be a case of difficulty in mating associated with the size difference, but it may equally well be based upon a marked difference in temperament. It has been very noticeable that while all the island stocks become relatively docile, *britannicus* remains extremely wild and shy and difficult to handle even after many months in captivity.

The emphasis here upon the "sterility barrier" is explicable when Steven later says, "I do not now think we can reasonably regard [the Hebridean populations] as more than well-differentiated subspecies." Evidently his criterion for the species gap is more strict than is customary, for, if his limited observations are borne out, a rather distinct reproductive barrier may well separate the peripheral populations from the mainland ones, but possibly not from each other.

Steven apparently rejects the "relict" theories advocated by Hinton and by Zimmermann to explain the peripheral and alpine distribution of the "*nageri* group" forms, but his reason for doing so is never explicitly stated, at least so far as I can tell. He prefers to believe in a polytopic origin of the three peripheral British strains "during the past few thousand years from a common stock with *C. glareolus britannicus*," but he does not support this belief with significant evidence. It seems to me that Steven's data, admittedly still preliminary in 1953, do more to support the relict theory than to oppose it.

My friend Dale Osborn tells me that cases of central-peripheral distribution of characters may not be rare in small North American mammals. He instances the northern shrews of the *Sorex arcticus-tundrensis* complex, which may represent a single species. The shrews from Nova Scotia and Alaska tend to have light brown backs and light buffy sides, while those from southern Labrador and central Canada are dark- or blackish-brown on the back and light brown on the sides.

Bipolar Distributions of Marine Animals

Certain distributional phenomena found among marine animals may indicate that central-peripheral speciation is active in the sea. Numerous interesting cases are mentioned by Ekman (1953, pp. 249–263) in his very full discussion of *bipolarity*, a term that covers the distributions of species (or genera and families) with ranges in higher latitudes of both Northern and Southern Hemispheres, but which do not occur in intervening warmer zones. Sometimes the same or "twin" species or genera have a bipolar distribution, and related species or genera fill in through the tropical seas between, a condition Ekman calls "masked bipolarity."

> There is among the Challengeriidae (Radiolaria) a deep-water form, *Protocystis sloggetti*, which is mainly domiciled in the equatorial oceanic regions of the Atlantic and Indian Ocean between 40° N. and 40° S. and may be caught most frequently between 400 and 1500 m. In cold seas, in the north as well as in the south, it is replaced by the distinctly bipolar *P. harstoni*, which is common in these seas and which prefers the upper layers of water, although it has also been found alive at a depth of 4000 to 5000 m. *P. harstoni* has probably developed in both the cold-water regions by adaptation to similar environmental conditions from an equatorial ancestral form, closely related to or perhaps identical with *P. sloggetti*. . . .
>
> A similar explanation may, according to Michaelsen, be given for the position of two independent although very closely related species of ascidians, namely *Botrylloides leachi* and *B. nigrum*. The former occurs in the North Atlantic (Norway to Mediterranean) as well as in the southern hemisphere off South Africa, West Australia, New Zealand and the Aucklands, while *B. nigrum* lives in the tropical part of the East and West Atlantic, the Indian Ocean and the West Pacific.

In still other cases, such as that of the foraminiferan *Globigerina pachyderma* and its tropical form *dutertrei*, similar bipolar types are clinally linked to intermediate tropical populations and are thus demonstrably conspecific. Ekman feels that these examples arise through "*bipolar taxonomic parallel development*."

What percentage of such cases is genotypically, not phenotypically, determined is at present uncertain. Among the genetically based cases independent (polytopic) origin and parallel evolution of some bipolar characters under the pressure of similar cold-water environments is of course one possibility. Another possibility is that the bipolar populations represent the peripheral relicts of an

old, widespread population that has undergone a central change or suffered central replacement (Théel, 1886; Strohl, 1936).

CONCLUDING DISCUSSION

The most significant parts of the hypothesis are the emphasis on the center as the principal source of evolutionary change leading to "potent" new species and higher categories, and the role of population density fluctuations in spreading characters and making and breaking the contacts between populations.

As has already been emphasized, there is nothing new in the idea of evolution by central change, and centrifugal spread of change. I have already suggested that even if we assume a species range within which there exists complete uniformity of environment, population density, and distribution, and rate of spread of different adaptive genetic changes—even then we can expect a differential to develop between the geometric central and peripheral areas of the range (see Fig. 1).

When we substitute a natural species distribution for such an ideal model, the irregularities introduced are of overriding importance so far as the origin and spread of genetic change are concerned. However, it seems that these irregularities even more strongly favor differentiation of central from peripheral populations, provided that we now think of "central" areas primarily in terms of their overall carrying capacity and reliability as permanent breeding grounds, rather than in the narrow geographical sense. Of course, where there is no serious asymmetry in the positions of the physical and biotic barriers determining the distribution of the species, we expect to find reasonable correspondence between the two kinds of centers—geographical and evolutionary. This correspondence is apparent in several of the examples discussed. In cases where distributional limits are asymmetrically placed, such as those in which the most favorable part of the breeding range of a terrestrial animal is close to one coast of a continent, or crowded by high mountains, the evolutionary center may seldom be near the geographical center of the range. In this sense, species ranges are probably more often asymmetrical than not.

Despite asymmetry, the active evolutionary center of a species range may often be located more or less exactly by observing relative population densities at different points, by determining the source or direction of any emigrations, and by plotting the geographical variation of the species and the ranges of related species. One expects this center to be both broad and indefinite, and to have had a history of shift and change.

The currently favored models of geographic isolation leading to species separation are those involving simple division of the range and colonization across barriers. While no doubt simple division and colonization processes can and do lead to specific separation, it is difficult to regard species that may have been formed in one of these ways as the main source of further evolution.

Probably the division type of speciation is exemplified most often by the east-west species pairs in Eurasia and North America, thought to be the resurgent survivors out of Pleistocene refugia. The trouble with such cases is that many of them can be interpreted in alternative ways (Mayr, 1942, pp. 177–180). There often is no good reason why such species pairs may not represent two waves of populations coming from the same direction.

Colonization speciation has been discussed by Mayr (1942), especially under the heading "Double Invasions" (p. 173). The concept of double invasion has much in common with the present hypothesis, except that Mayr seems to stress differentiation of the insular isolates rather than of the continental source populations.

Mayr later (1954) developed the colonization idea into his hypothesis of "typostrophic" speciation, which emphasizes the probability of marked changes in the selective value of genes against the altered "genetic environment" of peripheral colony-founders as compared to that of the source populations. In this way, the aberrant nature of some peripheral populations is accounted for, and Mayr suggests that these populations may represent one kind of situation from which new major groups of animals arise. [It is unfortunate that Schindewolf's term "typostrophic" has been brought into speciation discussions and somewhat fixed there (e.g., Hubbell, 1956). Mayr, of course, was using the term in a way very different from the way in which Schindewolf employed it.]

"Typostrophic" changes may occur and may be important in colonial speciation, but it is necessary before accepting Mayr's idea to review the facts and theories bearing on insular colonization and evolution.

It seems likely that Mayr over-minimizes the importance of biotic differences between some of

the islands he discusses as populated by colonists. In particular, it is important to ask how the potential competitors and predators of a colonized island compare in numbers and variety with those of the source area and other islands. Lack's work on the Galapagos finches (1947) should demonstrate that this question is of the utmost importance in studying insular variants, and should also prove that it cannot be answered merely by citing general environmental similarities between ranges of different populations.

Further difficulties in Mayr's typostrophe theory have already been mentioned in the introduction. Criticism may be summarized here by saying that this kind of typostrophic change remains to be convincingly demonstrated as an important factor in the evolution of insular species, and that in any case it seems unlikely to have been of much significance as a source of new major groups that are capable of sustained invasion and radiation back into continental areas.

Fortunately, we can learn something about major-group evolution by looking at the distribution of the groups themselves. Following the surveys by P. J. Darlington (1948, 1957), we find that it is likely that most higher-category groups arose in continuous or near-continuous land masses with warm climates, and spread from there to smaller land areas or to those with less favorable climates. The Old World tropics apparently has been the largest of these favorable regions, and the one that has given rise to more dominant, world-spreading groups than any other, at least back through the Tertiary.

Darlington thinks that the large warm areas probably owe their evolutionary potency in large part to their greater chances of producing *general adaptations*—character combinations that confer upon a species the competence to enter a wide variety of environments and prosper in most.

I feel that Darlington's ideas and my own are directly complementary, though we are interested in different levels of the evolutionary hierarchy. If major-group evolution is only the extension and accumulation of normal speciation sequences, as at this moment seems to be the general consensus, then there is no occasion for surprise at the similarity of the central-peripheral patterns produced by the two processes. The only difference expected and found is one of scale.

In order to avoid a misunderstanding of one important point, it may be necessary to re-emphasize, first, that the argument presented above is an argument for an hypothesis only, and an hypothesis that requires a great many more facts for its eventual proof or disproof; second, that the kind of speciation here argued is not the only one possible—rather, I think of it as the approximate means by which are produced the species most likely to participate in general phyletic advances.

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NEW BIOLOGICAL BOOKS

The aim of this department is to give the reader brief indications of the character, the content, and the value of new books in the various fields of Biology. In addition there will occasionally appear one longer critical review of a book of special significance. Authors and publishers of biological books should bear in mind that THE QUARTERLY REVIEW OF BIOLOGY *can notice in this department only such books as come to the office of the editor. The absence of a book, therefore, from the following and subsequent lists only means that we have not received it. All material for notice in this department should be addressed to H. B. Glass, Associate Editor of* THE QUARTERLY REVIEW OF BIOLOGY, *Department of Biology, The Johns Hopkins University, Baltimore 18, Maryland, U. S. A.*

THE ORIENTATION OF BIRDS

BY DONALD R. GRIFFIN AND CHARLES G. GROSS

Biological Laboratories, Harvard University

Being a review of BIRD NAVIGATION.

By G. V. T. Matthews. Cambridge University Press, New York. $2.50. viii + 141 pp.; ill. 1955.

In recent years scientists have shown renewed interest in one of the central problems of animal behavior, the orientation of birds. G. V. T. Matthews, whose own experiments have played a leading role in this resurgence of interest, has reviewed the facts and theories concerning the sensory basis of bird navigation. This book, the third in the Cambridge Series of Monographs in Experimental Biology, goes on to present a new theory. The hypothesis which Matthews advances as a complete, if tentative, explanation for bird navigation is summarized by him as follows: "The essential feature is the *sun arc*. This is inclined at an angle from the horizontal which is constant for a given place and is a measure of the latitude of that place. . . . The speed at which the sun moves round its arc, is, for practical purposes, constant, at 15° an hour. When it has reached a particular point on its arc at home, it will have advanced further to an observer in the east, and less far to one in the west, the difference in arc angle (the angle round the arc from the noon position) being directly proportional to the change in longitude. At home the bird will become familiar with the features of the sun arc, and the sun's position on it at different (local) times. These will be related to the internal 'chronometer' which is also an essential part of the hypothesis. In unfamiliar surroundings the bird will have to construct the sun-arc from observation. The suggestion is that it observes the sun's movement over a small part of its arc and extrapolates to obtain the highest point. Measurement of the altitude of this point, the angle from the horizontal, and comparison with the remembered value for home, say, the previous day, will give the latitude change. The arc angle from the observed sun to this highest point when compared with that obtained at home for the same chronometer time will give the longitude change."

The reality of a complete form of navigation (Type III of Griffin, 1952) seems to be adequately established by Matthews (and by Kramer, 1952), at least for Manx shearwaters and homing pigeons. For example, a Manx shearwater released near Boston, Mass., returned to its home off the coast of Wales in twelve days. Even more impressive are the clearcut demonstrations by Matthews and Kramer of the ability of Manx shearwaters and homing pigeons to direct their flight homeward within a minute or two after being released in unknown territory. The homing speeds of these individual birds indicate a fairly direct flight route in contradistinction to the homing performances of many other species of wild birds and other colonies of homing pigeons. In the past, poorer homing performances (i.e., slow homing speed and low percentages of returns) in overcast weather have suggested that the sun is involved in bird navigation. Recent experiments by Matthews and Kramer have confirmed the importance of the sun, by demonstrating that birds which show correct homeward headings when released in clear weather scatter almost at random under cloudy skies.

There are two experimental approaches to the testing of Matthews' hypothesis: (1) measurement of the sensory abilities assumed to be involved in detecting the astronomical phenomena; and (2) experimental manipulation of the postulated environmental clues. Matthews does not emphasize the point that the path of the sun's apparent movement will be perceived as a circle only if the bird refers it to something other than the surface of the earth, for example, the position of the north star, or the plane of the ecliptic. The theory has been criticized by Kramer (1957) on this and several other grounds. Other possible and more probable ways of perceiving the sun's path (such as a change of the sun's altitude above the horizon with time or azimuth position relative to terrestrial landmarks)

would involve extrapolating along sinusoidal curves. These tasks of extrapolation past inflection points are rather more difficult than those that Matthews claims are essential in birds feeding on moving prey.

The proposed sun arc hypothesis demands of birds an exceptional visual acuity as well as an extremely accurate internal chronometer. Since homeward orientation has been shown to occur at all times of the day and within a few minutes after first seeing the sun, Matthews is postulating extrapolation from a small observed segment of the sun's path which may lie near the horizon and which may involve the sun's movement through only 2 or 3 times its own diameter. The only behavioral evidence that he brings to support this suggestion is Gundlach's report (1933) that one pigeon discriminated between horizontal and vertical lines subtending an angle of 23″. This value for the minimum separable acuity was obtained by selecting the best portions of each experimental run and subjecting only these to significance tests. Gundlach does not present the probability that one such "good run" would occur by chance in each of his series of tests. Even according to his calculations, the data indicating a visual acuity of 23″ show a standard deviation of 0.67 and would occur in unselected material 25 times in 100 tests. Subsequent more careful investigations of the visual acuity of the pigeon, none of which are cited by Matthews, have obtained values of 2.7′ and 7.8′ for the minimum separable acuity (Hamilton and Goldstein, 1933, and Chard, 1939). As in Gundlach's study these values were obtained from experiments in which the pigeon was required to distinguish horizontal from vertical stripes. It may be quite a different problem for a bird to judge with equal precision a large visual angle such as the altitude of the sun above the horizon.

Although the existence of an internal chronometer in birds and its importance for orientation have been established by recent experiments (Hoffman, 1953, and Rawson, 1954), whether or not these chronometers have the accuracy required by the sun-arc hypothesis is still an open question. As an indication of the requisite accuracy, it may be calculated that at latitude 50° an error of 5 minutes in the estimation of local noon would result in an error of 50 miles in judging longitudinal displacement.

Matthews attempted to demonstrate the validity of his hypothesis by indirectly manipulating the assumed environmental clues. To test the proposed method of latitude determination, he prevented pigeons from seeing the sun or sky for 6 and 9 days at the season of the autumn equinox. When the birds were first allowed to see the sun again at a release point in unknown territory its noon altitude had dropped about 2 and 3 degrees, respectively. The release point was about 1 degree south of home, so that the altitude of the sun would be expected to indicate a displacement to the north. Most of the birds did fly roughly south, as though misled by the change in the sun's altitude. However, 18 per cent flew north towards home. Matthews calls these "a better calibre of homers than the majority." Rawson and Rawson (1955) and Kramer (1952) have since repeated this experiment and obtained negative results; that is, a similar drop in the sun's latitude did not affect the bird's ability to select the correct initial heading and to home from unknown territory.

In an experiment designed to establish the importance of internal chronometers for avian longitude determination, Matthews subjected pigeons to an artificial day out of phase with the normal day, assuming that they would obtain incorrect information from the sun arc upon release, since their chronometers would be "reset." Most of the experimental birds did show a definite tendency to fly east after continued exposure to an advanced day, and west after exposure to a retarded one. Paralleling the case of the "superior homers" in the latitude determination experiment, 25 per cent of the pigeons exposed to a shifted daily cycle were apparently unaffected by these shifting attempts, since they homed at least as well as the control birds. Matthews suggests that these "superior birds" may have had more "stable chronometers." It is regrettable that Matthews did not record some other aspect of the birds' daily cyclic behavior, such as the amount of activity or time of free feeding, as an indication of the state of their internal chronometers, rather than use their orientation itself as the only criterion for reset chronometers.

This monograph is certain to stimulate further experiments on homing and migration. But the hypothesis it offers, although a definite advance over its predecessors, calls for the Scotch verdict of "not proven." A more complete discussion of Kramer's ideas on sun navigation would have added to this exciting, if slightly over-enthusiastic, little book.

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GENERAL BIOLOGY: PHILOSOPHY AND EDUCATION

INTRODUCTION TO BIOLOGICAL SCIENCE. *A Study of the Human Body and of the World of Plants and Animals.*

By Clarence W. Young, G. Ledyard Stebbins, and Frank G. Brooks; illustrations by Louise Bush. Harper & Brothers, New York. $4.75. xii + 555 pp.; ill. 1956.

The authors point out that this text is based on a considerably longer book, *The Human Organism and the World of Life.* The present edition is a completely rewritten and condensed version to meet the needs of a less detailed course in biological science. The fundamental aim of both books remains the same: to present the life processes of the human body and the relationship of man to the organic world. We therefore find that Part I is devoted to the human organism, with the usual systems taken up in an unusual sequence. At first reading, this new sequence makes sense; future study and trials may confirm this impression. A special chapter is devoted to the scientist and the scientific method and another to human diseases and their control.

Part II covers the plant and animal kingdoms, adaptations, communities, and evolution. Classification is practically non-existent, and details of morphology are omitted except when needed to illustrate an important phenomenon. At the close of each chapter there is a new summary outline, a set of questions, and a glossary of new terms. Numerous drawings (well-done), photographs (well-chosen), a list of references for outside reading, and a workable index round out the anatomical details of this book. It is lucidly written, and its organization shows clearly that the authors had a well-conceived objective which has been excellently carried out.

HENRI C. SEIBERT

BIOLOGY: HISTORY AND BIOGRAPHY

E. A. BIRGE. *A Memoir.*

By G. C. Sellery; with an appraisal of Birge the Limnologist, An Explorer of Lakes, by C. H. Mortimer. The University of Wisconsin Press, Madison. $3.50. viii + 221 pp. + 7 pl.; text ill. 1956.

When a historian who became a dean and then emeritus writes a memorial volume for a limnologist who became president and then emeritus, it is only fitting that the press of the university concerned should publish the volume. The present memoir arose in this way.

To many it will come as a surprise to learn that the man who discovered the thermocline (1897) and named the epilimnion and hypoliminion (1910) was in 1873 assigned the task of classifying echinoderms by Louis Agassiz—the last year of the great naturalist's life. For most persons, E. A. Birge stands as the author of the chapter on Cladocera in Ward and Whipple's *Fresh-Water Biology* (1918) and as coauthor, with Chancey Juday, of nearly 1,500 pages of fine limnological research reports between 1921 and 1941.

For biologists, the final chapter and selected bibliography by Mortimer will have particular appeal, since they identify Birge's contributions to the establishment of limnology as an important field of investigation. Birge concentrated his attention on the lakelets of Wisconsin, particularly Lake Mendota, and tried to make quantitative measurements which would describe accurately the varying conditions of the environment for plankton organisms. He was most successful when attacking well-defined problems, and contributed greatly to an understanding of the penetration of sunlight, the heat budget, and the chemical changes characteristic of small lakes. Since larger bodies of water, such as nearby Lake Michigan, had little attraction for him, he may have overemphasized the differences between limnological matters and those of concern to oceanographers.

Long after administrative commitments had curtailed the time Birge could spend in the laboratory during the academic year, he continued to devote summer vacations to explorations in lake-studded Wisconsin. In his eighty-ninth year, limnologists from all over the world assembled to honor him. This was in 1940, a year before the appearance of the last two large limnological reports of which Birge was coauthor and a full decade before his death.

LORUS J. & MARGERY MILNE

BIOGRAPHICAL MEMOIRS OF FELLOWS OF THE ROYAL SOCIETY. *Volume 1, 1955. A new series in continuation of Obituary Notices of Fellows of The Royal Society, Vols. 1–9 (1932–1954).*

The Royal Society, London. 30s. vi + 263 pp. + 17 pl.; text ill. 1955.

This volume is a continuation of the nine volumes of F.R.S. obituaries which appeared between 1932 and 1954. Nineteen biographies are presented, each by a scientific associate of the Fellow who is the subject of the piece. A photographic portrait of each Fellow is included, and a complete list of his publications accompanies most of the essays. Albert Einstein, Enrico Fermi, and Stafford Cripps are included in the current volume. (Cripps did brilliant chemical research in his early years, but later abandoned science for the law and public life; he was elected a Fellow of the Royal Society in 1948 in recognition of his "conspicuous service to science" while a member of the government.)

Most of the authors obviously have expended great care in the preparation of the biographies. Each reader will find certain ones particularly interesting. My own favorites are the biographies of Wood Jones and Arthur Keith, both of them by Le Gros Clark, and that of Edward Mellanby, by Sir Henry Dale.

As a final note, it may be added that the physician-reader (indeed any reader) cannot fail to be distressed at the waste of brain-power represented by premature deaths, such as those of Fermi and of Turing, the mathematician.

VICTOR A. MCKUSICK

BIOGRAPHICAL MEMOIRS OF FELLOWS OF THE ROYAL SOCIETY. *Volume 2, 1956.*

The Royal Society, London. 30s. 345 pp. + 23 pl. 1956.

Twenty-two biographies of recently deceased Fellows are presented here. As in the case of Volume 1, each is well-written and accompanied by a portrait of the man concerned. Readers will enjoy the diverse fields represented. My own favorites among the pieces were the biographies of Anrep, by Gaddum; Oswald T. Avery, by Dubos; and both Alexander Fleming and Robert Williams Wood, by Diecke. Pfeiffer—a student of Robert Koch—who discovered the Pfeiffer bacillus and was a foreign member of the Royal Society, is the subject of another interesting biography.

VICTOR A. MCKUSICK

LANCET. *A Novel.*

By Garet Rogers. G. P. Putnam's Sons, New York. $4.50. 448 pp. 1956.

"Certain critics of no little discernment," wrote André Gide, "have considered that fiction is history which *might* have taken place, and history fiction which *has* taken place." While it is not the usual custom of this journal to notice novels, some questions concerning *Lancet* warrant space in these pages. This book, a novel based on the lives of John and William Hunter, sticks closely enough to reality to seem more like inaccurate history than invented fiction. Is fiction an echo of facts, as Geoffrey Scott has called it? and if so, to what degree is it permitted to distort? How far do biography and history themselves also misrepresent character? The blurb on the jacket of *Lancet* concludes by saying that all the principal facts and characters of this novel are taken from life. Does literature *take from* or *contribute to* life? And which does history do?

The novel has received rather cursory reviews as fiction in the Sunday Book Review Section of the *New York Times* and in London (where it was published under the title *Brother Surgeons*) in the *Times Literary Supplement*. Since the British reviewer has testified particularly to the accuracy of the novel, it becomes appropriate to inquire into the veracity of a conception which portrays William Hunter as very nearly a fop, John Hunter a sodden wastrel, and Anne Home Hunter an icy-hearted social climber.

Looking back at the 18th Century from the vantage point of the 20th, it is all too easy to drift into a revery which paints London as an idyllic haven, more tranquil and leisured and verdant than we see it today, and to forget the lice and the gin, the stench and the cries in the streets, and the shouting throngs at Tyburn. All these unlovelier aspects of London, as the background to the life of the Hunters, the novelist has described with what can only justly be called great vividness. A sociologist might say, I suppose, that on the cultural level the novel is accurate; also, in the use of medical terminology the author is satisfactorily knowing.

It is specifically with reference to the lives of the Hunters and other members of their circle that the author's fidelity to fact must be challenged. She clearly has an intimate acquaintance with the literature about them: she puts into their mouths quotations which

their contemporaries have cited directly, and she has incorporated into the dialogue sentences and phrases out of their published writings or letters. The general chronology of the events of their lives bears resemblance to the actual, although there are some deviations from it. Thus, the novel has John (who came to London at William's request, by the way, and not, as the author claims, on a brief visit before entering the army) making the distinguished dissection of the arm which first drew attention to his anatomical prowess within twenty-four hours of his arrival in London. To the best of my knowledge, no evidence exists as to the precise date of the dissection; that it was begun or completed so soon would seem unlikely, since dissection is a technique which, like writing novels, often takes some learning.

Perhaps the date of the dissection is not a "principal fact," in the words of the jacket; perhaps it is of no importance to the writer or the reader of the novel whether the dissection was made a day or a week or a month after John's arrival in London; and perhaps many other apparently minor deviations from known fact are equally without weight. It may well be without major import that Anne Hunter's brother-in-law, Robert Mylne, is mentioned in connection with the building of Westminster Bridge, although it was his design for the bridge at Blackfriars which brought him fame. There may be two opinions of the permissibility of altering facts in time and space in order to enhance the dramatic value of a novel based on the lives of actual individuals called by their real names. There may be less room for argument on the justifiability of erroneous interpretation of real characters.

The author assumes that a somewhat ambivalent relationship between the Hunters is explanatory of much of their conduct, and there is no doubt that much is to be said for such a stand. But the contrast between the characters of the two brothers is exaggerated beyond all meaning. William had some vanities, to be sure, and probably many more than John; he was probably more devious than John, as I myself once marshalled some evidence to suggest. But this is not the same as saying that a primary basis for the rift between them was William's arbitrary action in a scene over a crone's granddaughter who was warming his bed. William Hunter was human too. If there is no evidence for the existence of Polly and for her residence in the house in the Great Piazza, there is none specifically against it. It is hard to say, after an interval much shorter than 200 years, whether or not it is in character for a man to have had his way with a particular maid. It is possible, however, to say that from the known records it seems highly out of character for William to have quarrelled with John over a Polly, just as it is unlikely that the author has correctly represented William's reply to John's remark that they were brothers. " 'Yes,' William said, basking in the shadow of his wine, 'incredible, isn't it?' " ("Shadow of his wine," indeed; William is recorded by his contemporaries to have enjoyed a glass of claret, but he is also described as very nearly ascetic in habit.) It is inconceivable, in the face of the known evidence, that he could have said of John, even to their sister Dorothea, that "he is vile and disorderly. He is a hopeless wastrel, a drunkard," or that he should have called John to his face "a wastrel who destroyed flesh, and let it rot and putrefy."

In fact, the primary effort of the novel is to describe John as a drunken debauchee, at least during the twelve years he spent in London prior to his departure for the Peninsular War. He is said to have had his bottle of wine "ever to hand as he worked," and to have gone on "an orgy of sluts, appeasing and satiating where there was not appetite;" and long, degrading episodes are recounted in which he fell into violent depravities. Again, there is no documentary evidence to demonstrate conclusively the exact manner in which John spent his hours in London when working or playing. He is known only to have enjoyed the theater, a form of recreation probably too pure to be mentioned in the novel as one of his indulgences. The author herself admits her lack of evidence in a note preceding her prologue: "If John Hunter's twelve-year 'London season' was not exactly as we find it here—the facts are lost—still, this could have been the way of it."

More will be said shortly as to why this could not have been the way of it, but what of the later years, the years of his long engagement and of his marriage, and what of his wife, the former Anne Home, and their relationships to each other and to their friends? John Hunter, who was an honest man, had his enemies during his lifetime, as honest men often do; yet even Jesse Foot, the most pusillanimous of them, could find nothing to criticize in Anne. The portrayal of Anne as loath to marry John until she had despaired of Joseph Banks ("John looked on in pain and humiliation while Anne made a fool of herself over Joseph Banks"), and as having named their first son for Banks, are equally without basis of fact. In contrast, the strong bonds, both personal and professional, between John Hunter and Joseph Banks are very well known. The improbability that Banks should have said to John, "Were you to fall at my feet in a spasm this moment, I do not think I would lift a hand to save you," is matched only by the impossibility that Anne could have said to him, "You ugly little man with your thick features and your vile person! You smell of death, John Hunter. You smell of death and blood. You are crude and virtually unlettered, you dance as a sow might staggering in her wallow, and when you touch me I see the collection of rotted flesh and filth under your nails. You are an abomination of a man, John Hunter."

Gentle, mild Anne! It seems even more cruel to darken her memory fictionally than that of her husband. She left behind her only a small literary heritage and a good repute, which, because of her very delicacy, have faded with the years into obscurity. John's character, in

contrast, still speaks for itself, in so far as his work speaks for him.

The author of *Lancet*, near the end of her novel (pp. 437–441), presents a straight-forward list of subjects of John's professional interest—a little over four pages of solid print, interrupted by one indentation for a new paragraph. What will this convey, to the ordinary reader, of the nature of the work of the man who has been defamed through all the preceding pages? It is not only in the sheer quantity of his output that John proved himself to have been otherwise than here portrayed, but in its quality—its courage, its vigor, its vision. Perhaps, in the back of factual data, it seems arbitrary in a number of cases to question Garet Rogers' interpretations; but that Hunter's work was accomplished by a man of soundness and more than normal energy, of integrity not only in the sense of honesty but also of consistent wholeness, is a judgment maintained for more than 150 years by those who have known his work well and who have built upon it.

W. H. Auden has written recently in a review of a biography of Housman that that poet "was one of those rare people whose skeleton, so to speak, was always showing, and this is just what a novelist finds stimulating, a solid ground upon which he can build the body of his imaginary details." John Hunter's skeleton always showed, too, and it was strong; there should have been no problem to clothe it with healthy flesh. Garet Rogers has lacked eyes to see it; the bare bones of John Hunter's character were curiosity, enthusiasm, imagination, and strength, not weakness; and his whole surgical and scientific accomplishment attest to these. Such intellectual vitality and power as were his could never have been generated by dissipation.

Never having considered myself fiction-minded, it had never occurred to me to think of the Hunters as good subjects for a novel. In fact, they are ideal. If we assume that the motive of the author was to write a good novel, it is easy now to see how much better she could have done it had she delineated accurately, rather than perverted, their true natures. Consistency is at least a partial measure, I believe, of the success of fictional characterization.

The author can of course use the defense that she writes fiction, not fact. If fiction is what is fabricated, how far is it fiction when it deals with known and named individuals? The historical novelist is confronted by the same difficulty as any historian or any biographer: in the face of incomplete records, what are the possible interpretations of the facts at hand? Facts can sometimes be verified, but who can verify human motives? From this point of view all biography may be suspect. How can we be sure of the motives of those who lived two centuries ago, when we can hardly know those of our friends, or even our own? There can be no certainty, but there must be serious effort to follow where the evidence seems to lead. In so far as history must be the master, not the servant, of the biographical novelist (recently remarked by Irving Stone, who addresses an audience similar to Rogers'), the novelist is as reprehensible as the false historian if he contraverts what evidence is available. By falsifying the characters of some admirable men and women, Garet Rogers has done a great disservice, not only to the memory of the individuals and to herself, but likewise to the cause of historical fiction in a period when it is vigorously attempting to set for itself new literary and historical standards.

JANE OPPENHEIMER

ECOLOGY AND NATURAL HISTORY

AN ECOLOGICAL GLOSSARY.
Compiled by J. Richard Carpenter. Hafner Publishing Company, New York. $5.75. x + 306 + xxiv pp.; ill. 1956.

This glossary appeared in 1938 and was not impressive then. C. Stuart Gager (*Ecology*, 19: 482) in a review stated, "This book will serve a valuable purpose if it emphasizes the need of a reliable glossary. . . . Beginners in ecology ought to be forbidden to use the book." Since nothing has been added to it, the book has only historical interest. Indeed, the references end with 1935—and by 1957, so many new terms and usages have appeared that the glossary is quite useless. Even the author's main definition, "Ecology—the science of communities," is no longer valid.

DAVID E. DAVIS

THE ORNITHOLOGISTS' GUIDE.
Edited by H. P. W. Hutson. Philosophical Library, New York. $10.00. xix + 275 pp.; ill. 1956.

Major General Hutson, Chairman of the British Trust for Ornithology, has compiled a series of short articles by 46 authors, including himself, in an attempt to direct the enthusiasm of British amateur ornithologists into channels that would further our knowledge of bird life. He has made a special effort to encourage interested individuals who find themselves in foreign countries and free enough to make worthwhile original studies or to compile data suitable for comparison with data of other students.

The book is divided into the following nine main topics: General, Geographical Aspects, General Behaviour, Breeding, Protection, Study Techniques, Suggestions for Special Study, Regional Information, and General Information. By far the most useful of these topics, in my opinion are the Study Techniques and Regional Information. The former includes information about choosing field glasses, tape recording in the field,

automatic recorders at nests, bird trapping, ringing (banding), hides (blinds), surveys and censuses, nesting records, skinning techniques, parasite studies, and night observations. Since the average length of the articles is only 3½ pages (some illustrated), complete treatments are not to be expected. But special references are listed after most of the subjects.

Under Regional Information there is a compilation of the names and addresses of ornithologists, societies, collections, and sanctuaries, as well as lists of reference books and check lists for many parts of the world. The faunal regions most thoroughly covered are the Ethiopian, the Oriental, and the Australian; but the Neotropical, Arctic, and Antarctic regions are also included. The listings for each area do not pretend to be complete or entirely up to date; but there are some obvious omissions for the Neotropical region, the area with which I have myself some familiarity. Such important works as Eisenmann's *Annotated List of Birds of Barro Colorado Island, Panama Canal Zone*, published by the Smithsonian Institution in 1952, and *The Species of Middle American Birds*, published by the Linnean Society in 1955, definitely should have been included. Chapman's voluminous work on the birds of Columbia is also missing, along with Dickey's and van Rossem's monograph on the birds of El Salvador.

Turning to the book as a whole, most of the articles are written in such an elementary style that they seem to belong to the same author. Certainly only a very inexperienced person would profit by reading it from cover to cover. If Major General Hutson had addressed a more experienced audience, with the same well-founded intentions, the book would be more stimulating to the amateur ornithologist, whether a beginner or not.

WILLIAM B. HEED

THE DESCENT OF PIERRE SAINT-MARTIN.

By Norbert Casteret; translated by John Warrington. Philosophical Library, New York. $4.75. xii + 160 pp. + 16 pl.; text ill. 1956.

The Gouffre de la Pierre Saint-Martin is the second deepest cavern studied by speleologists. It opens close to the Spanish border in the Basque country of France and for two years was famous as the tomb of Marcel Loubens, who fell to his death in it in 1952. Casteret's first 98 pages, with accompanying diagram and illustrations, tell of explorations to the 2,389-foot level and recreate the difficulties of raising Loubens' body to the surface in 1954.

The remainder of the book deals far more briefly and less vividly with other European caves Casteret has explored. The book's greatest attraction for biologists may be the final 11-page chapter on The Little People, which tells of bat-banding, including a mention of the recovery of Rhinolophs H.057 and G.106 fifteen years after attachment of their wing markers.

LORUS J. & MARGERY MILNE

A NATURALIST IN PALESTINE.

By Victor Howells. Philosophical Library, New York. $6.00. 180 pp. + 29 pl. + 1 map.; text ill. 1957.

In 166 pages of text, Howells hurries the reader through an incredible assortment of animals, Arabs, flies, plants, and vagaries of weather. No less than 235 members of Palestine's fauna and 29 of her flora are introduced, many of them several times, and most of them by scientific name. For a nine-month sojourn in so small a country, this is a respectable list; but at better than three new kinds introduced on every two pages, the pace becomes a strain. Moreover, the animals are hard to tell from the people, since most of them seem filled with malice: the camel, the chameleon, the lizard, the robberfly, and the scorpion are all "angry;" and "hate" is the characteristic of the many poisonous snakes. We gather that big, black, fat flies make Palestine unbearable by day, and that a good night's sleep is rarely permitted by the migrating fleas, raiding rats, and sudden sandstorms. Even the author must have been reluctant to reread his book; for *Belostoma*, whose "cruel" claws grasp a luckless *Cyprinodon cypris*, according to the caption to a sketch on p. 82, is referred to as a "Water Beetle" there and in the index, but as "really a member of the Rhynchota" on p. 156. Howells has, however, provided a fresh natural history of Palestine.

LORUS J. & MARGERY MILNE

BEAUTÉS DU FOND DES MERS.

By J. Forest. Librairie Larousse, Paris. 1,575 fr. 104 pp.; ill. 1955.

Handsome photographs, in both black-and-white and color, make this a book to exclaim over. Monsieur Forest has provided a pleasant text and good captions to accompany the illustrations by Paul Popper, Quilici-Ravelli, Gunter Sennft, Steiner, L. Trabut, Woody Williams, Douglas P. Wilson, and by Scaloni who has taken a large number especially for the book at the aquarium in Monaco, at the British Museum (Natural History), and at the Muséum National d'Histoire Naturelle. A few other photographs were provided from the files of the Shedd Aquarium. Most of the fishes and invertebrates depicted are identified by scientific name, and all but a few were photographed from life. That the descriptive matter is in French may puzzle some parents whose children are filled with questions from

studying the fine pictures, but the attractiveness of the book as a coffee-table adornment should not be decreased by this feature.

LORUS J. & MARGERY MILNE

EVOLUTION

THE GREAT CHAIN OF LIFE.
By Joseph Wood Krutch; illustrated by Paul Landacre. Houghton Mifflin Company, Boston. $3.75. xiv + 227 pp.; ill. 1957.

Joseph Wood Krutch's books are always a pleasure to read. It makes little difference whether he is considering his fellow men and their aesthestic achievements, or whether, as in this book, he contemplates the meaning of life in all of its varied aspects; in any circumstance he shows a keen sense of observation, a sound and broad knowledge of his subject, and a deceptively simple but most apt turn of phrase. In *The Great Chain of Life*, he is concerned with the problem of evolution and with the personal question, "What am I?" that inevitably arises. With clarity and sureness of touch, he traces some of the aspects of evolution, and lays particular stress on the problem of sex. But Krutch is not content with mere descriptions; he is ever concerned with those qualities which we tend to associate uniquely with man: pleasure, exuberant joy, freedom of choice, awareness, mother love. He finds these as evident among the animals he knows as in man, and in a pure and uncomplicated form. From these considerations, and others as well, he would therefore insist that life is uniquely unlike anything found in the physical and chemical world, that it cannot be explained in physical and chemical terms, and that to say that something is alive is to say that it has a "soul."

Krutch feels that this point of view is unorthodox, in so far as current biological thinking is concerned, and that it cannot be encompassed by current evolutionary thought. I cannot but disagree with him on the latter point. Problems of "purpose," "fitness," and ethics must of course be raised; but while evolution embraces all such questions and must eventually provide an answer, it is not necessary to inject "will" or "preference" into evolution in order to make sense of life. Mr. Krutch's understanding of "survival" and "natural selection" is certainly not in the Darwinian tradition; he sees materialism as an anachronism which went out with the explosion of the A-bomb (why precisely then is somewhat obscure, since Einstein's equation clearly shows the interconversion of energy and matter); and he considers it "a staggering proposition . . . that chemicals which are merely material should come to understand their own nature."

The proposition advanced by Mr. Krutch that "the organization of atoms into nonliving material does differ radically from the kind of organization which results in living matter" is, in one sense, a meaningless statement, since it cannot be converted into a question to be asked of nature with any surety of an answer with verifiable connotations. In another sense, it is quite incorrect if one takes into account the recent viral studies of Fraenkel-Conrat or the nucleic acid work of Ochoa or Kornberg. I fail to see, furthermore, how Krutch derives comfort for himself and meaning for the concept of "choice" from the physicists discovery that, while masses of matter may, because of statistical probability, behave in a predictable manner, the individual atom is unpredictable. Surely this is grasping at straws in the manner of Sinnott. Is it not far better to assume that man is standing on that rung of the evolutionary ladder from which he can look back and comprehend what has taken place in the past? and that, because of this comprehension, chance has been in part replaced by choice? or that, superimposed upon a biological evolution, there is a cultural evolution that has led to the development of an awareness of self, an ethical framework for social behavior and individual action, and a set of values which man has created for himself? There is nothing in the history of science or culture which points to the fact that life, as an evolutionary phenomenon, has purpose. If there is any meaning to human existence it is because man has invested himself with purpose, including the ideas of good and evil, beauty and ugliness, harmony and disproportion. This is just as much a part of evolution as the development of a bird's song or the fragrance of a rose. It is an integral, and to man, a critically important link in the great chain of life.

C. P. SWANSON

SCIENCE AND THE LOVE OF GOD.
By Frank J. Pirone. Philosophical Library, New York. $4.25. xl + 233 pp. 1957.

F. J. Pirone is a Catholic, a medical man, and apparently something of a psychiatrist. Part I of his book, addressed to a hypothetical youngster named Tommy, is an attempted explanation of some of the mysteries of this perplexing world. Religion, medicine, biology, psychiatry, and other topics are mingled in a most surprising fashion. Poor Tommy gets so stiff a dose that a second psychiatrist might conceivably be needed to correct the confusion produced by the first one.

Pirone does not believe in plain ordinary evolution (p. 27); he prefers instead to interpret biological phenomena in terms of "parallel evolution," abbreviated as "paravolution." This makes the author more comfortable, since he can now explain the similarities between man and animals by "paravolution" along parallel lines of development. He commits an injustice, however, by declaring (p. 27) that "old Professor Darwin and many other later scientists thought men

came from monkeys." Again, on p. 192, we read that "Charles Darwin invented a hypothesis based on his erroneous conception that man descended from monkeys." Such an ignorant misinterpretation might be expected from some fundamentalist follower of William Jennings Bryan a third of a century ago, but it scarcely befits a writer who has pretensions to education and who is attempting to improve the knowledge of the young. In Darwin's *Descent of Man* and related works by other evolutionists, the only similar statement made is that man, apes, and monkeys very probably descended from a *common* ancestry.

On the other hand, Pirone lays himself wide open to counterattacks by the evolutionists (and others) in presenting a theory that before Adam and Eve there was no sex in the world (p. 102). "This means that symbiosis existed between the protohuman species which was paravolving." To give the process in slightly more detail, "Every prehuman creature attached to every other prehuman creature forming from mud, received sufficient water-food from total environment so that new individuals were continuously reproduced by all without one [sexually] 'knowing' one another." This sounds a bit like the process of budding which occasionally occurs in some protozoa or other single cells. If our interpretation is a fair one, perhaps we can call it the hypothetical protozooid stage of human reproduction, so that "Pirone's protozooid postulate" can now be presented to the confused mind of mankind to supplement—possibly to displace—Darwin's alleged monkey theory.

As a medical man, Pirone has a good deal to say about cancer, which, in his interpretation, seems to be approximately equivalent to melanoma. At any rate, he keeps harping on nevi, or "beauty spots," on the skin. These may lead to cancer, which in turn (in rather hazy fashion) is associated with the biological processes leading to old age and death. Altogether, there is not much hope for us, since we are told (p. 45) that "to discover the cause of cancer you must know the entire history of mankind from the time man was the slime of the earth to man as he now is." We have always heard that cancer is a difficult pathological problem, but never before that it is really a historical problem!

After apparently allowing Tommy to go his way, the author proceeds to Part II of his book, which is mainly an exposition of his understanding of the current Catholic position of psychotherapy. Sigmund Freud is belabored for his errors, but perhaps he can be extended a partial pardon. Pirone's book was not available to him, and besides he was sadly misled by Darwin's theory of evolution (p. 192).

The book is a sincere and earnest effort, but not a coherent or a successful one. If it does not quite fall under the category of eccentric literature, it certainly borders closely on that field.

WALTER C. TOBIE

LIFE, MAN, AND TIME.

By Frank Lewis Marsh. Pacific Press, Mountain View, Brookfield, Omaha, Portland. $2.50. 200 pp. 1957.

After reading the attempt by Frank J. Pirone (see the preceding review) to provide a Catholic interpretation of biological and medical science, it is interesting to turn to the similar attempt of a Protestant. F. L. Marsh is a Ph.D., not an M.D., and a Professor of Biology at Emmanuel Missionary College, Berrien Springs, Michigan. As such, he sticks pretty closely to an attempt to harmonize current conceptions of biology, in a general sense, with the Bible as he interprets it. Though the author's denominational affiliation is not stated, internal evidence suggests that it (p. 28) might be with the Seventh Day Adventists

As is usual in works of this sort, poor old Charles Darwin receives some heavy verbal hammering, which we will not detail here. In a general way, Marsh tends to accept the *data* of paleontologists and other biologists, but rejects their evolutionary *interpretations*. Instead, he goes to great lengths to explain the data in terms of the Bible, with particular emphasis on the book of Genesis. Anyone who accepts the evolutionary theory as being highly probable, at the very least, must regard such interpretations as more surprising than successful.

Since Marsh gives particular attention throughout his book to the story of Noah's ark, a few samplings of his thought on this early experiment in marine navigation are in order. Since he disregards the geological periods accepted by the majority of biologists, he has a very serious problem in deciding what Noah did about the dinosaurs. He concludes (p. 84) that Noah probably provided space in his ark for "forms like *Compsognathus*, which was no larger than a rooster." On the other hand, the big clumsy brutes like *Diplodocus* and *Brontosaurus* had to sink or swim. There was just not enough space for them in the ark; and, furthermore, they might become pests in the post-diluvian era by knocking down houses! This sort of reasoning (if one can call it that) puts Marsh in much the same category as the magazine and newspaper cartoonists who also discard geological periods in their thinking and insist on dragging in the dinosaurs of vastly earlier times to harass and annoy their comic-strip cavemen (as if the latter were not already busy enough belaboring each other with huge clubs)!

Marsh rejects the theory of some more moderate Bible students that Noah's flood was a "very local affair in the Mesopotamian Valley" (p. 86). He insists that it must have covered the whole earth; but, despite valiant attempts, he does not quite succeed in explaining where all that water finally went.

Though I will no doubt be accused of cynicism, I shall risk the following analogy. Most attempts to reconcile science with literal interpretations of religious doctrine remind me of the efforts of some inmate of an

institution, who has mixed together the pieces of two different picture puzzles, to piece them into a single unified whole. The pieces just don't fit! We have no solution to offer for this sad situation. Though we can observe such efforts with a certain sympathy, we can seldom agree that the resultant hodge-podge of discordant elements is worthy of any great attention, or even of very much respect.

WALTER C. TOBIE

TREATISE ON INVERTEBRATE PALEONTOLOGY. *Part V: Graptolithina with sections on Enteropneusta and Pterobranchia.*

Directed and edited by Raymond C. Moore. Geological Society of America, New York; University of Kansas Press, Lawrence. $3.00. xviii + 101 pp.; ill. 1955.

This small volume, written by an excellent specialist on the graptolites, comprehends whatever is remarkable about that extinct paleozoic group of animals. Problems of the systematic position and the reasons for including that class in the subphylum Stomochorda, which also includes the classes Enteropneusta (recent only) and Pterobranchia are discussed. Specifically concerned with the Graptolithina are such topics as: preparation, mode of life, significance of enclosing facies, geographical and geological distribution, mode of building, ontogeny, and evolutionary trends. Taxonomically, the Graptolithina are divided into the sessile (or encrusting) orders Dendroidea, Tuboidea, Camaroidea, Stolonoidea, and the epiplanktonic Graptoloidea. The division into Axonolipa and Axonophora, maintained still in the *Traité de Paléontologie* of C. Dechaseux (1943), is abandoned.

The book is very well illustrated with numerous enlarged and very clear line drawings. (The methods of graptolite illustration and their difficulties are discussed on pp. 14–15.) A glossary of morphological terms, lists of unrecognizable genera, and the more important references are also at hand. One may truly state that this volume is one of the best and most valuable of the published parts of the *Treatise on Paleontology*.

H. HÖLDER

REVISION OF THE JURRASSIC AMMONITE FAUNA OF MOUNT HERMON, SYRIA. *Bull. Amer. Mus. nat. Hist., Vol. 108, Art. 1.*

By Otto Haas. American Museum of Natural History, New York. $4.00 (paper). 210 pp. + 30 pl. 1955.

Since the treatment of the Mount Hermon Ammonites by Noetling (1887) the material representing that Lower Oxfordian fauna has become far more complete. It is now more than 50 times as abundant as that on which Noetling based his monograph. The fauna includes the families Phylloceratidae (4 species), Haploceratidae (*Lissoceras erato*), Oppelidae (*Hecticoceras*, by far the most abundant genus; *Ochetoceras; Taramelliceras; Creniceras; Scaphitodites;* in all, 21 species and almost 5000 individuals), Cardioceratidae (1 species), Perisphinctidae (13 species, 1936 individuals), and Aspidoceratidae (9 species).

Haas's descriptions of the species are extraordinarily exact, detailed, and complete, with many measures of sizes and proportions in millimeters with two decimal places (is that not an exaggerated refinement?). Photographic figures, often enlarged, are also given—mostly to illustrate various individuals and the ontogenetic stades of a single species. Fourteen species, or a little more than one-fourth of the total, are new; and two of them are not yet denominated (nomenclatura aperta).

The conclusions concerning the precise composition of the ammonite fauna and observations bearing on their ontogeny, phylogeny, evolution, and paleoecology are informative. *Aspidoceras*, and more particularly its subgenus *Euaspidoceras*, is considered an offshoot from the Perisphinctidae by way of *Mirosphinctes*, and *Taramelliceras* an offshoot from *Sowerbyceras*. Some species of quite different genera show remarkable homeomorphies and convergences which excite the special interest of the author. The environment of that mostly pyritized ammonite fauna is believed to have been neritic. The apparent dominance of small species can be explained for the most part by their incompleteness (preserved inner whorls of larger specimens). But there are also many nearly complete shells, mostly of juvenile individuals that can be sufficiently accounted for by heavy infantile and juvenile mortality.

The author is right to feel that all the new supraspecific names created in the last half century are a burden; but even he applies *Richeiceras* (as a subgenus of *Taramelliceras*) although it "seems to be one of the most readily dispensable" terms.

HELMUT HÖLDER

GENETICS AND CYTOLOGY

ADVANCES IN GENETICS. *Volume VIII.*

Edited by M. Demerec. Academic Press, New York. $9.00 x + 402 pp. 1956.

Half of the present Volume VIII of *Advances in Genetics* is devoted to excellent reviews of basic research in genetics; the remainder, to the genetics of certain economically important animals and plants. Francesco D'Amato and Otto Hoffmann-Ostenhof trace the search for mutagenic substances within higher plant cells from the early observation of De Vries, that stored, aged seeds show a higher spontaneous gene mutation rate in

Oenothera lamarckiana than fresh seeds show, to the identification of a number of naturally occurring metabolites which cause gene mutation and chromosome breakage in various plants. Sometimes these substances are automutagenic; i.e., they affect the plant species in which they are found. The concentration of such metabolites increases with age in *Soja hispida*. These mutagenic substances have no doubt contributed to the spontaneous mutation rate of higher plants during the course of evolutionary development.

Verne Grant has analysed the various genetic systems that differentiate the races and species of *Gilia*. Since he concludes that the same types of genetic systems and isolating mechanisms are at work differentiating races as are found differentiating species, he favors the view that there has been a gradual evolution of the species from the race.

The same author, in Chromosome Repatterning and Adaptation, discusses the suppression of recombination in structural hybrids, a suppression that causes the locking up of adaptive gene complexes. This process has favored the production of new plant species through hybridization. In structural homozygotes, polygene complexes may be retained intact through chiasma localization. Grant points out that the prevalence of chromosome repatterning in many different plant and animal groups shows its basic importance. Even the mutation rate can be affected by structural change. Position effects involve a direct relationship of chromosome repatterning to the phenotype. Future studies will reveal possible adaptive position effects.

Taku Komai's Genetics of Ladybeetles is especially interesting because of the vast amount of early work which has been done in an attempt to explain the geographical variation of the elytral pattern in these insects. The author reviews work on the stable polymorphism in a number of *Harmonia* and *Adalia* species showing major multiple allelic genes to be responsible for certain patterns. The minor variations in spots and elytral pattern found in *Epilachna* and *Hippodamia* are polygenic in origin. Consideration is also given to the effect of environmental conditions on the elytral pattern in lady beetles. Of special interest is the temporal variation extending over a period of forty years in a population of *Harmonia axyridis* in or near the Japanese town of Suwa, a work in which Komai coauthored with Chino and Hosino.

The volume contains four papers on plants and animals of economic importance. These appeal to me because of the challenge that confronts the worker who deals with such genetically difficult organisms as the bee or the sheep. Warwick E. Kerr and Harry H. Laidlaw review the great advances in bee genetics made possible by the development of a successful artificial insemination technique perfected in the late 1940's. The evolutionary features of nest-making, storage of food, control of colony temperature, and swarming are traced among the three social tribes of Apidae.

A. L. Rae reviews the inheritance of various color and pattern characters in sheep fleece, growth and body conformation, fertility, and milk production among the various breeds of domestic sheep. Although a number of monofactorial traits are known in sheep, the important productive traits are multifactorial. Furthermore, since the diploid chromosome number is 54 or 60, linkage groups are not yet identified and no fully established case of linkage exists. Hence geneticists have to depend on statistical procedures as aids in selection for economically desirable traits. The development of the various kinds of hairs in the sheep fleece has been thoroughly worked out in order to evaluate the heritability, separately, of such characters as hairiness, fiber diameter, number of crimps per inch, quality number, staple length, and face cover. Crossbreeding has long been carried on in sheep in order to form new breeds and to produce fat lamb and mutton. Inbred lines are now being systematically developed in an effort to see if results in sheep can approximate the great success obtained in breeding corn.

Charles M. Rick's and L. Butler's review of the Cytogenetics of the Tomato is one of the most stimulating in the volume. The identification within the past six years of each of the 12 haploid chromosome types has made it possible to assign linkage groups to definite chromosomes by the trisomic method. The authors present a description of 129 tomato mutants not previously published. The use of species hybridization in the genus *Lycopersicon* to introduce disease-resistant genes into various tomato races represents a great genetic achievement, from the economic point of view. The reviewers discuss the excellent suitability of the tomato for studies of graft relationships, for host-pathogen relationships for virus diseases, for biochemical studies, and for studies of dominance and heterosis. Here is a plant with rich possibilities for studies of basic problems, although it is at the same time of great economic importance.

H. H. Flor's review of the host-parasite relationship between cultivated flax, *Linum usitatissimum* L., and its rust, *Melampsora lini*, is extremely important—not only for its value to flax-growing, but also for its implications as to future genetic methods of controlling rust in cereals. The author sets forth the hypothesis that for each gene-conditioning rust reaction in the host, there is a specific gene-conditioning pathogenicity in the parasite, and that these complementary genic systems in both flax and flax rust are responsible for the pustule type on the flax. The use of tester host stocks, homozygous for single rust-conditioning genes, to identify the number of virulent genes in the parasite is a generally applicable method.

For the reader who wishes to know what is being done in genetics throughout the world, the present volume

quite literally gives the answer. Its contributors come from Canada, Italy, Austria, Brazil, Japan, New Zealand, North Dakota, and California.

SARAH B. PIPKIN

INTERCROSSING AMONG PINK CALLA, WHITE-SPOTTED CALLA, AND YELLOW CALLA.

By Ryohitsu Shibuya; translated by G. T. Neichi. Tokyo [order from author, 1430 Grant Road, Mountain View, California]. Free upon request. iii + 57 pp. + 27 pl.; text ill. 1956.

This little book includes the results of ten years' work in breeding three species of calla—*Zantedeschia rehmannii*, *Z. albomaculata*, and *Z. elliottiana*—by a Japanese plant breeder living in California. It is neatly prepared, with full text and tables in both Japanese and English, and is profusely illustrated with photographs and color prints.

The parent plants used in these experiments were obtained through inbreeding for several generations. The author observed no noticeable deterioration after repeated self-fertilization. The reciprocal crosses between the white-spotted calla, the yellow calla, the pink calla, and their progenies are outlined in Chapter III; and the segregations of the observed characters in height, leaf-shape, leaf spot, and spathe color in the F_1, F_2, and F_3 generations are tabulated in Chapter IV. Unfortunately, a considerable number of segregated progenies, especially those of cross-breeding by the yellow calla, are eliminated in the experiments because of the low viability of seed, albinism, or susceptibility to disease.

The author concludes that the occurrence and expression of anthocyanin color in the calla depend on the complementary effect of four pairs of dominant genes. The variation in color intensity suggests the presence of suppressors for the anthocyanin coloration (Chapter V).

The genes for yellow color are found to be independent of those for the anthocyanins. The absence of yellow color in F_1 progenies of yellow × pink and pink × yellow crosses indicates either the recessive nature of the yellow genes or the coexistence of dominant genes and suppressors. The hypothesis advocated by the author assumes the presence of complementary genes which give rise to the suppressing effect on the expression of yellow color.

WANG CHI-WU

GENETICS NOTES. *Second Edition.*

By James F. Crow. Burgess Publishing Company, Minneapolis. $2.50 (paper). iii + 124 pp.; ill. 1955.

Those teachers of genetics and, even more, those students of the subject who are unacquainted with this collection of "notes" and problems are missing an invaluable aid. For clear exposition and for succinct coverage of almost every aspect of the field, this unassuming publication far excells many textbooks of genetics. The author's eminence and his experience in both Drosophila and human genetics are a sufficient recommendation. Sections on human genetics include chapters on Blood Groups, Twins: Heredity and Environment, and portions of chapters on Selection and Eugenics, Quantitative Inheritance, and many other topics. The scope of the manual is indicated by the inclusion of chapters on Multiple Alleles and Pseudoalleles, Cytoplasmic Effects, the Genetics of Bacteria and Viruses, Population Genetics, and Genetics and Evolution. None of the more usual topics is slighted. A very useful statistical appendix contains a treatment of the Chi-Square Method, Confidence Limits for the Binomial Distribution, and Measurement Data. The answers to the abundant problems supplied with every chapter are to be found at the end of the book. All righthand pages are left blank for taking further notes. In short, genetics is thrice blessed by having such an aid to students, and other branches of biology may well be envious!

BENTLEY GLASS

LES CRAPAUDS, LES GRENOUILLES *et Quelques Grands Problèmes Biologiques. L'Avenir de la Science, 38.*

By Jean Rostand. Gallimard, Paris. 750 fr. (paper). 216 + ii pp. + 48 pl. 1955.

Les Crapauds, Les Grenouilles et quelques grands problèmes biologiques, by Jean Rostand, is a volume in the series *L'Avenir de la Science*, edited by the same author. The great biological problems which Rostand discusses in connection with his own investigations on frogs and toads relate, in one way or another, principally to genetics. He presents brief chapters on parthenogenesis, gynogenesis, sperm conservation, and nuclear transplantation; but the major portion of the book is devoted to analysis of some hereditary syndromes, of which polydactyly represents the primary symptom. By far the greater part of the material covered is the author's original work, much of which has apparently not been published in more technical publications. The book has a double purpose: it presents the author's own descriptive and experimental data; and from these, it attempts to draw generalizations couched in popular terms to illustrate for non-specialized readers the processes of biological investigation. While the book differs in both outlook and style from most of the biological literature examined in this country by young students or laymen, reading it might prove salutary as

a reminder of the fact that simple study of field organisms and the simplest types of laboratory experiments can illuminate significant contemporary problems that are often less directly attacked in modern laboratories. Rostand is a distinguished and successful scientific popularizer in his own country; but while his presentation is luminous to those who know French well, it is highly idiomatic, so that some American readers will require more than a dictionary to appreciate it fully. All the more reason for them to read it!

JANE OPPENHEIMER

PROBLÈMES DE STRUCTURES, D'ULTRASTRUCTURES ET DE FONCTIONS CELLULAIRES. *Première Série. Exposés Actuels de Biologie Cellulaire 1955.*

Edited by J. André Thomas. Masson & Cie., Paris. 3000 fr. (paper). viii + 358 pp.; ill. 1955.

This volume is comprised of a group of papers based on lectures delivered at the Sorbonne in the spring of 1954. The Growth of Crystals and Assimilation, by J. Barraud; Recent Concepts of Enzymatic Mechanisms, by R. Wurmser; and The Form of the Desoxyribonucleic Molecule, by L. R. Rey, are devoted primarily to a study of physical factors of import to cellular biology. Problems more strictly at the level of cell biology are discussed in Structure and Permeability of the Cellular Membrane, by D.-G. Dervichian; in Cellular Adhesion and Morphogenesis, by Ch. Devillers; in Intertissue Junctions by R. Couteaux; in Ultrastructures and Functions of the Neuron, by A. Fessard; and in The Ultrastructure of the Cancer Cell, by Ch. Oberling and W. Bernhard. A paper follows on the Survival of Spermatazoa and Conservation of Their Powers of Fertilization, by C. Thibault; and the volume concludes with a discussion by R. Coujard of Histological Effects at a Distance of Limited Lesions of the Peripheral Sympathetic System. In the name of the series, the word "actuels" carries a connotation of present timeliness not implied by its English counterpart. Since these presentations were in 1954 and 1955, both the *Quarterly Review of Biology* and I owe apologies to the publishers for the tardiness of this comment. The articles are thoughtfully conceived and thoughtfully presented throughout, and can be read with value by students of cellular biology both now and for a good while to come.

JANE OPPENHEIMER

GENERAL AND SYSTEMATIC BOTANY

A GLOSSARY OF MYCOLOGY.

By Walter H. Snell and Esther A. Dick; illustrations by Henry A. C. Jackson. Harvard University Press, Cambridge. $5.00. xxxi + 171 pp. + 15 pl. 1957.

Great difficulty in understanding mycology is due to the extensive specialized vocabulary of the subject. The present volume was created to alleviate this difficulty. It represents an enlargement upon Snell's *Three Thousand Mycological Terms*, published in 1936. Approximately 7,000 terms drawn from the literature of mycology and related fields, such as medical mycology and antibiotics, are included. Terms used in several standard works to designate colors have been translated into their nearest equivalent in the widely available *Color Standards and Nomenclature*, by Ridgway. Fifteen plates by Henry A. C. Jackson illustrate terms concerned with morphological characters of fungus fruiting bodies and spores. The volume should be a useful reference and source book to workers in the mycological field.

F. T. WOLF

A MANUAL OF SOIL FUNGI. *Revised, second edition. By Joseph C. Gilman. The Iowa State College Press, Ames.* $7.50. x + 450 pp. + 13 pl.; text ill. 1957.

The second edition of this popular treatise on the fungi of soils is, like its predecessor (*Q. R. B.*, 20: 384. 1945), an attractive, carefully organized volume. As in the first edition, a key to the families of soil fungi is followed by keys and technical accounts of classes, orders, families, genera, and species. One or more line drawings, set into the text, illustrate the main features of each genus; and 13 excellent and informative photomicrographs are tipped in at the back. A list of pertinent literature referred to in the body of the text, a glossary, an index, and a very sketchy general account of the fungi complete the volume.

As indicated by the author, this is a compilation of soil-fungi descriptions and records from all parts of the world. Since the last edition (1945), 32 genera and 142 species have been added. Plant and animal parasites have been excluded for the most part, as outside the scope of the manual.

That there can be no doubt of the usefulness of such a manual as this is indicated by the need for two reprintings of the first edition. Just how complete and authoritative the whole is cannot be judged by any single mycologist, for the book covers the Phycomycetes, the Ascomycetes, and the Moniliales. In my own field of interest, the zoosporic Phycomycetes, a confused picture is presented. For example, as in the previous edition, only two soil chytrids are included. In reality, many representatives of various genera of these fungi have been described from soil, particularly by Harder and his students. Again, in the treatment of the Blastocladiales, although Couch's and Whiffen's

species of *Blastocladiella* are included, so is the genus *Sphaerocladia*, which was placed in synonymy with *Blastocladiella* by these authors in a paper describing their species! Further, the cut illustrating *Blastocladia* shows a fungus long since removed from that genus. To describe the chytrids in the key to the classes, orders, and families as being oosporous, and the gametes of the Blastocladiales as differentiated into eggs and sperms, will prove a sore strain on the morphological conscience of discriminating mycologists. Nonetheless, if I find a queer fungus in soil, I will turn first to Gilman's book—except, of course, if the fungus belongs to my own group.

F. K. SPARROW

CONE-BEARING TREES OF THE PACIFIC COAST. *Fifth Printing, in which is included new material on An Introduction to Tree-Ring Analysis.*

By Nathan A. Bowers. Pacific Books, Palo Alto. $3.50. xxxvi + 169 pp.; ill. 1956.

This is an exceedingly well-organized and informative manual of Pacific Coast conifers and is designed for the use of people unfamiliar with the technical terminology of the botanical taxonomist. Unlike many efforts at popularization, the descriptions of needles, cones, and bark presented here are not sketchy and generalized. The illustrations for each species include the excellent drawings of needles, cones, and seeds first published in G. B. Sudworth's *Forest Trees of the Pacific Slope*. In addition, half-tones of bark and mature trees for each species are presented. The author has prepared three rather unique keys based on (1) needles, (2) elevation, and (3) geographical distribution. An introductory chapter is devoted to an Introduction to Tree-Ring Analysis which will be of interest to those readers whose fondness for trees is not limited to external morphology.

SCOTT S. PAULEY

ECONOMIC BOTANY

BIOLOGY AND CONTROL OF THE SMUT FUNGI.

By George William Fischer and Charles Stewart Holton. The Ronald Press Company, New York. $10.00. x + 622 pp.; ill. 1957.

G. W. Fischer, well known for his previous work with the smut fungi, including publication of *The Smut Fungi: a Guide to the Literature, with Bibliography* (1951) and *Manual of the North American Smut Fungi* (1953), has combined forces with C. S. Holton, another prolific worker in the field, to prepare a comprehensive volume on all biological aspects of this interesting and important group of organisms. Of the 33 genera and 1162 species considered, it is estimated that approximately 900 would constitute valid species when, and if, a proper balance is struck between morphological and physiological characters in species delimitation. The customary division of the smuts into two families has been abandoned.

A thorough historical treatment of the smuts, and statistics showing the magnitude of financial losses for which they have been responsible, are presented. Numerous effects of infection that bring about morphological and physiological alterations in the host plants are detailed. In relation to their hosts, the smuts are classified into seedling infection, embryo infection, shoot infection, and local infection types. There are thorough discussions of life history, heterothallism and parasitism, and the growth of these fungi upon artificial media. Other chapters deal with cytology, hybridization, mutation, and genetics; and with the extensive variations encountered in these organisms both in the field and in the laboratory. Reactions of susceptible and partially susceptible hosts and the genetics of resistance on the part of the host are considered.

There is a discussion of the toxicity of smuts to animals and man, a problem to which no firm conclusion seems possible at the present time. A chapter is devoted to the methodology employed in spore germination studies, in inoculation, and in the determination of physiologic races and sex compatibility groups. A final chapter on control measures leads to the paradox that, while numerous instances of quite satisfactory control procedures have been worked out, these pathogens continue to exact a heavy toll and appear to be in no imminent danger of extinction through the efforts of mankind.

The book is well illustrated and unusually free of typographical errors. There is an extensive bibliography of 150 pages, covering a range of material from Tillet and Prevost to the present. The authors are to be commended for the preparation of a reference book on the biology of the smut fungi which is likely to be extremely useful for some time to come.

F. T. WOLF

PLANT PATHOLOGY. *Second Edition.*

By John Charles Walker. McGraw-Hill Book Company, New York, Toronto, London. $10.00. xi + 707 pp.; ill. 1957.

The first edition of J. C. Walker's *Plant Pathology* (*Q. R. B.*, 26: 400. 1951) has gained wide acceptance as a standard textbook in this important area. The subject matter of the second edition, like that of the first, is divided into 17 chapters. Following the introduction, there are chapters on the history of plant pathology; on non-parasitic diseases; on bacterial dis-

eases; and on diseases caused by Plasmodiophorales, Phycomycetes, Imperfect fungi, Ascomycetes, Basidiomycetes, phanerogamic parasites, nematodes, and viruses. Other chapters consider the relation of environment to disease development and host-parasite interactions. The concluding chapters deal with disease control through exclusion and eradication, protection, and host resistance. The 194 illustrations are well selected and of good quality, and the diseases and other materials dealt with are well documented by references to the original literature.

Since the first edition of this book has previously been reviewed, it would seem that the present review should most properly concern itself with the changes made in the second edition. Inspection reveals, however, that while some recent literature has been added to the new edition, the differences between the two editions are relatively minor and unworthy of detailed comment. It may be expected that the second edition will be as well received as the first.

F. T. Wolf

Forest and Range Policy. *Its Development in the United States. The American Forestry Series.*

By Samuel Trask Dana. McGraw-Hill Book Company, New York, Toronto, and London. $6.50. xii + 455 pp. 1956.

This book, designed primarily as a text or reference book for students of forestry and related fields of resource management, describes the development of forest and range policy in the United States from the colonial period to the present time. Particular emphasis is placed on the evolution of federal policies, since these largely reflect policy developments at state and lower governmental levels, as well as those of the private forest owner. The chapters are well organized, and the material is presented in a logical and even interesting manner. A summary and a selected list of references concludes each chapter. An appendix to the book provides a more general list of references on the broad subject of forest and range policy. Two other appendices provide a brief résumé of Federal policies dealing with other natural resources (wildlife, soil, water, minerals) and a chronological summary of major developments of policy concerning the conservation of natural resources in general. Biologists with an historical bent should find this volume interesting and profitable.

Scott S. Pauley

Forestry and Related Research in North America.

Prepared by Frank H. Kaufert and William H. Cummings for the Society of American Foresters, Forestry Research Project. Society of American Foresters, Washington. $5.00. viii + 280 pp.; ill. 1955.

This book represents the end-product of a study of forestry and related research in North America that was undertaken in 1953, on the 25th anniversary of the passage of the McSweeney-McNary Forest Research Act. The study was conducted under the auspices of the Society of American Foresters, the National Research Council's Division of Biology and Agriculture, and the Rockefeller Foundation. Objectives of the study were (1) to review the progress in forestry and related research (wildlife, range, watershed, and recreation) in North America during the past quarter-century, (2) to determine the present status of research by all agencies, (3) to assess the adequacy of present research, and (4) to formulate recommendations and goals for the next quarter-century. Supported by statistics that are interpreted in highly readable prose, the authors have accomplished these objectives. The report will be of interest to forest research workers and especially to those who are planning similar research work in forestry or related fields.

Scott S. Pauley

Advances in Agronomy. *Volume VIII.*

Edited by A. G. Norman. Prepared under the auspices of the American Society of Agronomy. Academic Press, New York. $8.80. xi + 423 pp.; ill. 1956.

Volume 8 of this series continues to maintain a high standard of excellence in both subject matter and writing skill. The main objective of discussing soil and plant relationships is clearly adhered to.

From the soils standpoint, such subjects as the use of anhydrous ammonia and molybdenum as fertilizers, chemical tests to determine the lime and fertilizer needs of soils, and organic soils are discussed. Crop subjects include tall fescue, winter hardiness in crop plants, and progress in grass breeding. Crops and soils are combined in a treatise on crop production and soil management in the Pacific Northwest, and in another on the mineral nutrition of corn as related to growing this crop.

While the subject matter is diverse, the articles are carefully prepared and provide thorough reviews. The high standing of the various authors adds to the value of this publication.

Gilbert H. Ahlgren

Soil Fertility.

By. C. E. Millar. John Wiley & Sons, New York;

Chapman & Hall, London. $6.75. xii + 436 pp.; ill. 1955.

The basic principles of soil fertility are discussed in this text prepared for advanced students of soil science and related fields. Emphasis is placed on information useful in solving crop-production problems, wherever found. Factors influencing crop growth are given major attention. These include soil chemistry, soil physics, soil microbiology, and plant physiology. The relation of light, temperature, moisture, soil organisms, and the colloidal soil fraction to plant growth and crop production is also considered.

The various plant nutrients and fertilizer elements are discussed from the standpoint of supply in the soil, losses by the soil, and additions from various fertilizers and other sources to the soil. The functions of the various plant nutrients in plant growth, and plant symptoms indicating deficiencies, are also reviewed.

In the latter part of the book, sources and management of organic matter and various rotations and farming systems employed in different parts of the United States are considered. Here also is a review of some of the old classical field experiments conducted at several Experiment Stations. Tabular data and a careful selection of illustrations increase the worth of the text. This is a valuable contribution to the literature on soils by an able and experienced scientist.

GILBERT H. AHLGREN

SOIL CONSERVATION.

By Sellers G. Archer. University of Oklahoma Press, Norman. $3.75. xxii + 305 pp. + 16 pl.; text ill. 1956.

The practical need for soil conservation and the methods whereby conservation may be achieved are emphasized here. The author has had broad experience and many practical and professional contacts in this field, and he presents his material in a skillful and easy-to-read manner.

Planning for soil conservation must be based on the needs of the land for prevention of erosion, for growing crops, and for soil improvement. Having established this, the writer discusses land capability maps and their interpretation, and the development and use of a conservation plan. The places for crop rotations, terraces, contouring, fertilizer practices, waterways, and other practices are elaborated in relation to conservation farming. The development and use of grasslands and their place in the overall scheme are also discussed. Farm forestry and wild-life on the farm complete the discussion of soil-conserving practices on the individual farm.

Pointing out that special practices may influence local farm units, the author discusses watershed protection and flood prevention, irrigation, and drainage. He stresses the value of these objectives and the techniques useful in securing them.

The latter part of the book is devoted to public assistance in conservation. Discussed here are local farm groups and their share in supervising and developing local programs. Agencies which give financial and technical assistance to the farmer are described, along with those which assist in education and research. The need for coordination of the various public assistance programs is stressed. This book will be of greatest use to those interested in the more practical aspects of conservation.

GILBERT H. AHLGREN

SOIL CONSERVATION.

By J. H. Stallings; foreword by R. B. Alderfer. Prentice-Hall, Englewood Cliffs. $8.50. vii + 575 pp.; ill. 1957.

The development of the soil conservation movement, its organization, and its accomplishments are here described by an able writer and scientist. Much experience and critical analysis of data were put into this easily read, well-organized book.

Divided into four parts, the book deals first with historical and geographical aspects of conservation. Part II considers water and wind as erosive forces; soil aggregates and the maintenance of soil structure; and the value and use of soil surveys, soil testing, and plant cover in conservation. In part III such general practices as relationships of land, plants, and animals; water and wind erosion control; mulch, grassland, and woodland farming; and other items are considered. The book concludes with a discussion of farm and watershed planning, including such subjects as land use capability, irrigation, drainage, and watershed management.

Those associated with soil conservation programs and interested in them will find this an interesting and stimulating book. Others will also benefit by gaining a clear picture of the importance of soil conservation to all of us, whether we live in the city, in urban areas, or on the farm.

GILBERT H. AHLGREN

GENERAL AND SYSTEMATIC ZOOLOGY

CALIFORNIA WASPS OF THE GENUS *OXYBELUS* (*Hymenoptera: Sphecidae, Crabroninae*). *Bull. Calif. Insect Survey, Vol. 4, No. 1.*

By Richard M. Bohart and Evert I. Schlinger. University of California Press, Berkeley and Los Angeles. 75 cents (paper). Pp. 103–134 + pl. 9–16; text ill. 1957.

This monograph provides a summary of the little that

is known of the biology of American oxybeline wasps, comments on their general distribution, a key to the 3 North American genera, and a key to the nearly 40 species of *Oxybelus* known from America and northern Mexico. Bibliographic, taxonomic, and distributional notes are furthermore given for the 24 forms now known (almost wholly owing to the efforts of the authors) from California, as well as distributional maps for the Californian forms, of which 5 appear endemic.

A frontispiece of a female *Oxybelus californicum* Boh. and Schl. illustrates the habitus of these wasps, and some 8 plates of morphological characters (chiefly postscutellum, squamae, and propodial spine) helpfully supplement and illustrate the long key to *Oxybelus*. By its comprehensive key, the monograph has country-wide usefulness; it may be expected to foster new interest in these curious little wasps, and no less to assure tidying up taxonomically long-neglected collections.

K. W. COOPER

NEARCTIC WASPS OF THE SUBFAMILIES PEPSINAE AND CEROPALINAE. *Bull. U. S. natl. Mus., No. 209.*

By Henry Townes. Smithsonian Institution, Washington. $1.50 (paper). iii + 286 pp.; ill. 1957.

With the appearance of Townes' fine monograph, the American spider-hunting wasps of the large family Psammocharidae (Pompilidae) are at last completely monographed. The work here under review, together with Hurd's (1952) treatment of *Pepsis* (see *Q.R.B.*, 28: 77–78), Bradley's (1944) revision of the Aporini, and Evan's (1950, 1951) exemplary monographs of the Psammocharini, collectively provide full systematic coverage and dissipate the taxonomic confusion that has plagued those persons seeking identifications for these wasps. Further generic refinement is perhaps to be expected within the Psammocharidae, but the species classification has at last been clarified and stabilized, and it is unlikely that a period of disorder can again prevail in the systematics of this difficult family.

As introduction to the monograph, Townes briefly discusses the status of the family name, the sources of the material studied, the terminology employed, and the major systematic divisions of the family which he reduces to three subfamilies: Pepsinae, Psammocharinae, and Ceropalinae. Townes' delineation of the validity of the family name Psammocharidae is brief and pointed, directly calling to task the International Commission on Zoological Nomenclature for recent arbitrary and unwarranted decisions, including that of the validation of the name Pompilidae. Thirty four photographs of wings (plates 1, 2), 14 photographs of male genitalia and subgenital plates (plates 3, 4), and 7 line drawings of morphology (fig. 1), provide such illustrations of anatomy as are required. The remaining 160 text figures are distributional maps for the species. Keys to genera (of which the second couplet of the key on p. 10 should read "*first*" instead of "*second* recurrent vein") and species are provided, generic and specific (for each sex where known) descriptions are given, and very full distributional records are listed. To these are added notes on dates of capture, on rearing records, on prey and parasites, and on such other biological information as is available. Some 22 species and 24 subspecies are described as new, and a number of new names are given. The text closes with two indices: one to the systematic names, the other to hosts, prey, and parasites.

Most biologists will never see, no less use, this admirable monograph. Yet, like other fine works of systematics, it will ultimately influence and lighten the tasks of many naturalists, animal behaviorists, and ecologists remote from the immediate field of systematic entomology. To authors of works such as this one, most modern biologists regrettably stand in unknowing debt.

K. W. COOPER

THE NATURAL CLASSIFICATION OF THE FAMILIES OF COLEOPTERA.

By R. A. Crowson. Nathaniel Lloyd & Company, London. 30s. viii + 187 pp.; ill. 1955.

While older classification systems of beetles were largely artificial, i.e., were based upon arbitrary characteristics, newer efforts have aimed towards a natural or phylogenetic system, in which the arrangement of families is supposed to correspond to their positions in the evolutionary scale. Almost all the evidence for these new classifications had to be obtained from the external and internal structure of the adults and the larvae. Paleontological remains of beetles are usually not sufficiently well preserved for the study of the necessary details.

The present volume gives a detailed account of the author's system of classification. While Crowson's system agrees in many essential features with those of other modern authors, it differs in numerous details. Crowson adds a fourth suborder Myxophaga, to the three which are usually recognized. As in other alternative systems, the bulk of the material (145 families out of a total of 161) is contained in the suborder Polyphaga, which is subdivided into 19 superfamilies. The author's attitude toward subdividing some of the larger families, such as the Carabidae, Scarabaeidae, and Chrysomelidae, is fairly conservative.

The classification given in keys to the suborders, superfamilies, families, and subfamilies in some cases cannot be used for identification as to families of every specimen. It was not meant to serve this purpose, but rather to bring out the general phylogenetic relation-

ships. In my own opinion, however, a dichotomous key is not the best way to represent such relationships. The author uses larval structure and wing venation, as well as the external and internal structure of the adult anatomy, throughout. Crowson believes that the primitive beetles originated in the Permian period, probably from the Neuroptera, and that they were fungus-eaters living under bark.

The book is not written for a beginner. It gives a thorough account of modern views of the classification and evolution of the Coleoptera. The examples are taken chiefly from British beetles but the coverage is world-wide. This volume should be a welcome addition to the reference works available to the serious student of insect classification.

G. H. DIEKE

THE OTIORRHYNCHINE CURCULIONIDAE OF THE TRIBE CELEUTHETINI (COL.).

By Guy A. K. Marshall. British Museum Natural History, London. 35s. (paper). 134 pp.; ill. 1956.

This book presents a revision of the weevils of the tribe Celeuthetini, found in the Pacific area between Australia and Java. A key to the 72 genera (30 of them new) accompanies the work; and there are descriptions of many new species, as well as keys to the species of a few genera. The excellent figures should be a great help in recognizing the species.

G. H. DIEKE

COLÈOPTÉRES CARABIQUES DU MAROC. *Zoologie, No. 1. Mém. Soc. Sci. nat. Phys. Maroc.*

By M. Antoine. Èditions Larose, Paris; Institut Scientifique Chérifien, Rabat. 680 fr. (paper). 177 pp.; ill. 1955.

THE MELIGETHES OF NORTH AFRICA (COLEOPTERA, NITIDULIDAE). *Mémoires de la Société des Sciences Naturelles et Physiques de Maroc. Nouvelle série, No. 2.*

By Alan M. Easton. Editions Larose, Paris; Institut Scientifique Chérifien, Rabat. 360 fr. (paper). 71 pp.; ill. 1955.

These two monographs treat parts of the North African insect fauna. The part on carabids leans heavily on Jeannel's treatment in Vols. 39 and 40 of the *Faune de France.* It contains the following families with keys to genera and species and illustrations of structural details, including the male genitalia: Paussidae, Carabidae, Nebriidae, Notiophilidae, Elaphidae, Cicindelidae, Slagonidae, Cymbionotidae, Scaritidae, Apotomidae, Broscidae, Psydridae, Trechidae, and Patrobidae. These families, often considered only tribes in the older treatment, form the first four of the six groups of Jeannel: Isochaea, Simplicia, Srobifera, and Stylifera.

The part on *Meligethes* gives keys and descriptions of the North African species of this very difficult genus, with details of genitalia and other structures.

G. H. DIEKE

A CLASSIFICATION OF THE FIRST INSTAR LARVAE OF THE MELOIDAE (COLEOPTERA). *Univ. Calif. Publ. Ent., Vol. XII.*

By J. W. MacSwain. University of California Press, Berkeley and Los Angeles. $3.00 (paper). vi + 182 pp.; ill. 1956.

In recent years many entomologists have come to believe that the larval characteristics of beetles may give a truer picture of their phylogenetic relationships than the characteristics of the adults. MacSwain's monograph describes the first instar larvae of 109 species belonging to 32 genera and uses the results for a revision of the classification of the family Meloidae. In this family the first instar larvae are usually very agile, in some genera attaching themselves to bees, while the later instars are parasitic on the contents of the cells of the bees' nests. In other genera the larvae feed on egg masses of orthopterans. A few notes on adults supplement the data on the larvae.

G. H. DIEKE

A REVISION OF THE EROTYLIDAE OF AMERICA NORTH OF MEXICO (COLEOPTERA). *Bull. Amer. Mus. nat. Hist., Vol. 110, Art. 2.*

By W. Wayne Boyle. American Museum of Natural History, New York. $1.50 (paper). Pp. 61–172 + 1 pl.; text ill. 1956.

Boyle's work provides a monographic treatment of the beetle family Erotylidae (without the Languriidae), a group for which no review has appeared since 1873. There are keys to the genera and species, detailed diagnostic descriptions, descriptions of the genitalia, biological and geographical data, notes on the types, and drawings of structural details.

A treatise like this one is bound to be widely used by experts and beginners alike. It is a pity that, for the benefit of the latter, no drawings of the complete insects were included.

G. H. DIEKE

BIOLOGY AND TAXONOMY OF NORTH AMERICAN BEETLES OF THE SUBFAMILY GEOTRUPINAE, WITH REVISIONS OF THE GENERA *BOLBOCERosoma, EUCANTHUS, GEOTRUPES* AND *PELTOTRUPES* (SCARABAEIDAE). *Proc. U. S. nat. Mus., Vol. 104. No. 3342.*

By Henry F. Howden. Smithsonian Institution, Washington. Free upon request (paper). Pp. 151–319 + 18 pl. 1955.

Howden's work is a monograph of the genera indicated, with keys to the species and a key to all genera of the subfamily. There is a thorough discussion of the structure of adults and larvae, of their biology, with many of the author's original observations, as well as data based on extensive material concerning geographical distribution. Several new species are described. The monograph is a very valuable addition to our knowledge of a part of our fauna, the previously available literature on which had long ago become obsolete.

Some recent revisions of the genera are not treated in detail in this paper. But with Wallis, 1928 (*Bolboceras = Odontaeus*); Cartright, 1953 (*Bradycinetulus* and related genera); and Olson, Hubbel, and Howden, 1954 (*Mycotrupes*), all the North American species of the subfamily Geotrupinae are now available in modern treatment.

G. H. DIEKE

CHECKLIST OF THE COLEOPTEROUS INSECTS OF MEXICO, CENTRAL AMERICA, THE WEST INDIES, AND SOUTH AMERICA, *Part 6. U. S. natl. Mus., Bull. 185.*

Compiled by Richard E. Blackwelder. United States Government Printing Office, Washington. $2.25 (paper). Pp. 927–1492 + vii. 1957.

The insects of South America are still very imperfectly known. Before Blackwelder's work appeared, progress had been greatly handicapped by the absence of a reliable catalog. For the beetles, it was necessary to have recourse to the more than a hundred volumes of Junk's *Catalogus Coleopterorum*. This work is out of the reach of most individuals and cumbersome, to say the least, even to one who has access to a good entomological library. Blackwelder's *Checklist* has brought long-needed relief. The first five parts of his work list every known beetle, systematically as to families and genera and alphabetically within a genus, with references (in code) to original descriptions and indications of distribution.

The present Part 6 gives the bibliography without which the references in the previous parts would have very little meaning. Great care has been bestowed on this bibliography to make it complete. It is meant to contain every paper applying directly to Latin American species as well as those general papers recognized as having useful implications in the study of the Latin American fauna. The 418 pages of bibliography are followed by a list of journals and their abbreviations (44 pp.), corrections and additions to Parts 1–5 (58 pp.), a list of the new names proposed in Parts 1–5, and an index of the genera and higher categories.

The now completed *Checklist of the Coleoptera of Latin America* has made the study of Latin American beetles immensely easier for everyone. It took tremendous patience on the part of the author to bring the project to completion; but more than that, it took good judgment to make the necessary corrections and additions. While there can be no question about the usefulness of the list, one cannot expect a work of such magnitude to be completely free of flaws. Specialists of particular groups may sometimes prefer different arrangements, but this can hardly be held against the author. In going over the material most familiar to me, I found only one omission—namely, *Hyperaspis propria* Kirsch (p. 448 of Part 3).

G. H. DIEKE

THE ORNITHOGEOGRAPHY OF THE YUCATAN PENINSULA. *Peabody Mus. nat. Hist., Yale Univ., Bull. 9.*

By Raymond A. Paynter, Jr. Peabody Museum of Natural History, Yale University, New Haven. $9.50. iv + 347 pp. + 1 folded map. 1955.

The Peninsula of Yucatan is considered to consist of the Mexican political divisions of Quintana Roo, Yucatan, and Campeche and their neighboring islands. Typically it is a low lying coastal plain which, in spite of its rather undifferentiated physiography, has a vegetation ranging from xerophilous scrub to high forest. Paynter recognizes three zones which he calls Scrub, Deciduous Forest, and Rain Forest, occurring, in the order indicated, roughly from north to south. About 4000 specimens from the Peninsula were studied and are discussed in the Annotated List. The general range of each species; the specimens examined or reported in the literature; the habitat; and general remarks on taxonomy, breeding, and other aspects of the ecology are included for each form. This list enumerates 429 species—or 487, with subspecies.

At the end, Paynter discusses the composition, distribution, and origins of these birds. Transients and breeding forms are listed, the latter according to major habitat preferences. The breeding avifauna is apparently composed of three elements: a group which ranges extensively on the continent, a group whose affinities are principally Antillean, and species indigenous to the Peninsula. The history of each of these groups is analyzed.

All of this information provides a most definitive treatment of the birds of Yucatan. And in addition to the bird material, there is a description of the climate, physiography, and geology of the region; a complete bibliography; a large map showing all localities mentioned; and an index.

HENRI C. SEIBERT

ASPECTS OF THE BIOLOGY OF *POMATIOPSIS LAPIDARIA* (SAY) (MOLLUSCA: GASTROPODA: PROSOBRANCHIA). *Misc. Publ. Mus. Zool., Univ. Mich., No. 100.*

By Dee Saunders Dundee. Museum of Zoology, University of Michigan, Ann Arbor. $1.00 (paper). 37 pp. + 14 pl.; text ill. 1957.

A CATALOGUE OF THE CERIONIDAE (MOLLUSCA-PULMONATA). *Bull. Mus. comp. Zool., Harv. Coll., Vol. 116, No. 2.*

By William J. Clench. The Museum of Comparative Zoölogy at Harvard College, Cambridge. 75 cents (paper). Pp. 121–169. 1957.

THE GENUS *TETRAGNATHA* (ARANEAE, ARGIOPIDAE) IN PANAMA. *Bull. Mus. comp. Zool., Harv. Coll., Vol. 116, No. 5.*

By Arthur M. Chickering. The Museum of Comparative Zoology at Harvard College, Cambridge. 90 cents (paper). Pp. 301–354; ill. 1957.

THE CULICINE MOSQUITOES OF THE INDOMALAYAN AREA. *Part I: Genus* Ficalbia *Theobald.*

By P. F. Mattingly. The British Museum (Natural History), London. 8s. (paper). 61 pp.; ill. 1957.

REPORT ON A COLLECTION OF MARINE FISHES FROM NORTH BORNEO. *Fieldiana: Zool. Vol. 36, No. 3.*

By Robert F. Inger. Chicago Natural History Museum, Chicago. $1.00 (paper). Pp. 341–405; ill. 1957.

A SYSTEMATIC REVISION OF THE FISHES OF THE TELEOST FAMILY CARAPIDAE (PERCOMORPHI, BLENNIOIDEA), WITH DESCRIPTIONS OF TWO NEW SPECIES. *Bull. Brit. Mus. (nat. Hist.), Zool., Vol. 4, No. 6.*

By D. C. Arnold. The British Museum (Natural History), London. £1 (paper). Pp. 245–307.; ill. 1956.

STUDIES ON THE TRICHIUROID FISHES—3. A PRELIMINARY REVISION OF THE FAMILY TRICHIURIDAE. *Bull. Brit. Mus. (nat. Hist.), Zool., Vol. 4, No. 3.*

By Denys W. Tucker. British Museum (Natural History), London. £1 (paper). ii + pp. 73–130 + 1 pl.; text ill. 1956.

ECONOMIC ZOOLOGY

ATLANTIC COD TAGGING OFF THE SOUTHERN CANADIAN MAINLAND. *Bull. No. 105.*

By R. A. McKenzie. Fisheries Research Board of Canada, Ottawa. 95 cents (paper). viii + 93 pp.; ill. 1956.

INTERNATIONAL NORTH PACIFIC FISHERIES COMMISSION. *Annual Report for the Year 1955.*

International North Pacific Fisheries Commission, Vancouver. Free upon request (paper). 67 pp.; ill. 1956.

THE MARINE FISH CATCH OF CALIFORNIA, *for the Years 1953 and 1954 with Jack Mackerel and Sardine Yield per Area from California Waters 1946–47 through 1954–55. Fish Bull., No. 102.*

By The Staff of the Marine Fisheries Branch. State of California, Department of Fish and Game, San Pedro. Free upon request (paper). 99 pp. + 2 folded charts; text ill. 1956.

THE FIRST TEN YEARS OF COMMERCIAL FISHING ON GREAT SLAVE LAKE. *Bull. No. 107.*

By W. A. Kennedy. Fisheries Research Board of Canada, Ottawa. 50 cents (paper). vii + 58 pp.; ill. 1956.

ALASKA FISHERY AND FUR-SEAL INDUSTRIES, 1954. *Statistical Digest No. 37.*

By Seton H. Thompson. U. S. Department of the Interior, Fish and Wildlife Service, Washington. 35 cents (paper). iv + 70 pp.; ill. 1956.

ANIMAL MORPHOLOGY

INTEGRATED ANATOMY AND PHYSIOLOGY. *Third edition.*

By Carl C Francis and Gordon L. Farrell. The C. V. Mosby Company, St. Louis. $5.85. 641 pp. + 31 pl.; text ill. 1957.

This third edition of a successful textbook has been revised so extensively that a change in title appeared necessary. Earlier editions appeared in 1943 and 1950 (2nd Ed., *Q.R.B.*, 26: 215. 1951). The subject matter has been divided among more chapters, and the sections on physiology (which follow in each instance the discussion of anatomy, one organ system after another) have been completely rewritten to incorporate modern discoveries.

The authors, both medical men at Western Reserve University, have provided a high level, preprofessional human anatomy and physiology text with clear illustrations and few wasted words. Dedicated students will find its directness conducive to memorizing terminology and relationships, although they may discharge their course obligations without gaining much realization of the uncertainties and the continuing progress in these two integrated fields of knowledge.

LORUS J. & MARGERY MILNE

THE ORGANIZATION OF THE CEREBRAL CORTEX.

By D. A. Sholl. John Wiley & Sons, New York; Methuen & Company, London. $4.25. xvi + 125 pp. + 12 pl.; text ill. 1956.

Students and workers in any of the many fields concerned with properties of nerve cells will find this little monograph both provocative and profitable. The author has attempted "the presentation of a unified view of

some of the recent work that has been carried out by anatomists, clinicians, physiologists and psychologists in order to correlate the results of these various disciplines." Sholl's own work has led him to the statistical approach to problems of cortical organization and its relation to behavior and to properties of "mind." In one of the most stimulating sections of the book, he discusses the mathematical theories of cortical organization, and points out that "whether the cortex is studied by the anatomist, the physiologist or the psychologist, the model employed should be based on the concept of probability and discussed in a statistical language. This would imply that any theory that attempts to account for the properties of the dynamic spatio-temporal system that forms the basis of our behaviour must employ statistical hypotheses."

This kind of summary and philosophy should be of particular importance at the present time, when the investigative trend appears to be strongly directed toward a finer and finer analysis of "a neuron" or parts of a neuron, with relative neglect of the problems arising from the interrelationships of neurons in the aggregate. Perhaps this most intelligent and thoughtful monograph will give some pause to workers in this area and some new direction to their efforts.

R. G. GRENELL

THE SPINE. *A Radiological Text and Atlas.*
By Bernard S. Epstein. Lea & Febiger, Philadelphia. $16.50. 539 pp.; ill. 1955.

Though viewing the spine through a radiologist's eyes, the author does not limit his consideration of this anatomical unit to an interpretation of the various shades of gray it produces on an x-ray film. Instead, he presents the spine as a biological structure that is the subject of a wide variety of pathological processes, some primary to the spinal column, others secondary to systemic diseases. In addition, he presents those regional ailments, such as spinal cord tumors, that are brought to view by radiological procedures. It is not surprising, therefore, to find that the book treats a large number of diseased conditions, among them rheumatoid arthritis, osteopoikelosis, pilonidal cyst, traumatic avulsion of nerve roots, hemophilia, and other apparently unrelated conditions.

Quite properly the text begins with a survey of the embryology of the spine, the architecture of the spinal column, and a radiographic examination of the normal spine. The various affections are categorized in accordance with current concepts of their nature. For each affection, the author considers its etiology, pathology, and symptomatology, and records those changes that occur in the course of the disease. The manner in which the spine is affected is described; and the changes, as recognized in the radiological appearance, are presented. The differential diagnosis is not stressed, and treatment is only mentioned occasionally. In developing the presentation, pertinent discussions from the literature on the spine are offered. Occasional case reports make the reading lighter, while accounts of the author's personal experiences and expressions of his opinions give additional value to the presentations.

The text is liberally illustrated with photographs and reproductions of roentograms, yet the volume may be considered a textbook rather than an atlas. Although some sharpness has been lost in the process of printing, the illustrations are well chosen and well captioned. Judicious use of arrows considerably helps the reader to recognize points of significance.

This book is a valuable compendium of information. The subjects covered are numerous, and many of the affections discussed are rarely met by the clinician. One may expect, therefore, that the text will serve as a reference book to acquaint the reader with the various highlights of each disease of the spine. The extensive bibliography will prove to be of great assistance. Radiologists—and orthopedists, neurosurgeons, and others interested in the clinical aspects of the spine and its adjacent structures—will find this a valuable book.

I. WILLIAM NACHLAS

AN ATLAS OF ANIMAL ANATOMY FOR ARTISTS.
By W. Ellenberger, H. Baum, and H. Dittrich. Dover Publications, New York. $6.00. vi + 153 pp.; ill. 1956.

This cloth bound atlas of 151 pages contains an excellent bibliography; it is practical in size and lies flat when opened. To the painter, drawer, or sculptor of animals, it will be a much valued item. Illustrated in both line and half-tone, the plates are artistically beautiful and scientifically accurate. Aside from serving as a reference book, the volume will make one conscious of comparative anatomy.

Primarily, the topographical anatomy of the horse, dog, lion, and cow is treated, while that of the stag, roe goat, and cat are considered at less extent. Single pages are devoted to the monkey, seal, hare, rat kangaroo, flying squirrel, and bat—the purpose of these (presumably) being to prolong the romance of learning. This is the kind of atlas that one finds pleasure in using, though anxious all the while for the next edition.

WILLIAM E. LOECHEL

ANIMAL PHYSIOLOGY

PROBLEME UND BEISPIELE BIOLOGISCHER REGELUNG.
By R. Wagner. Georg Thieme Verlag, Stuttgart. DM 29.40. vi + 219 pp.; ill. 1954.

This work consists of a 31-page discussion of general theories about biological control systems and about 170 pages of examples taken from the control of the voluntary motor and cardiovascular systems of mammals. The theoretical material has a marked biological tendency and is not representative of current trends toward an abstract mathematical analysis of biological control systems. The section on the voluntary motor system does not treat of the recent studies of Kuffler in a degree comparable to their importance, nor does it integrate them into a general theory. This section does, however, give quite a good survey of earlier work in the field. The treatment of the cardiovascular system is also strong in classical material. A very interesting section is devoted to E. Koch's work on blood pressure and heart rate, work not well known in this country. The book as a whole is a useful collection of material on control of the two major systems mentioned, but it is not completely successful as a general synthesis in modern terms.

PAUL CRANEFIELD

ANNUAL REVIEW OF PHYSIOLOGY, *Vol. 19.*
Edited by Victor E. Hall. Annual Reviews, Inc., Palo Alto. $7.00. v + 639 pp. + 1 pl. 1957.

This volume continues the useful surveys for which the Annual Review series is well-known. Liljestrand, of the Karolinska Institut in Stockholm, provides the elder statesman's prefatory chapter. In recent years these wise observations on the past, present, and future of physiology have been an outstanding feature of the *Annual Review.*

I shall mention only a few of the 20 reviews presented, though all are equally significant. Barth of Columbia University discusses developmental physiology, i.e., embryology. Hypothermia, a matter of increasing interest to the physician, is discussed *in extenso* by Kayser of Strasbourg and, to some extent, in another review by Bělehrádek of London. Chenoweth and Ellman of the Dow Chemical Company review what progress has been made in the effort "to systematize the amorphous *logos* of pharmacology through researches in the chemistry of the drug-cell interactions." They have asked themselves, "What has this study contributed to the understanding of the intracellular events which cause the characteristic pharmacologic action of the drug under study?" Perhaps such a clear-cut objective makes their review particularly worthwhile. Mellinkoff of U.C.L.A. reviews the digestive system and provides a theory for appetite. Lysle H. Peterson of the University of Pennsylvania reviews the peripheral circulation, and Maurice B. Visscher and G. J. Stephens of Minnesota, the heart. Renal physiology is competently reviewed by Stanley E. Bradley of Columbia. An interesting feature is a review of recent advances in neurophysiology in Russia, prepared by Liberson of Northampton, Massachusetts.

VICTOR A. MCKUSICK

TEMPERATUR UND LEBEN.
By H. Precht, J. Christophersen, and H. Hensel. Springer Verlag, Berlin, Göttingen, and Heidelberg. DM 78. xii + 514 pp.; ill. 1955.

"Temperature is one of the most important environmental factors that influence life on earth." This thesis of the authors is generally accepted by biologists, as can be inferred from the widespread recording of temperatures in biological laboratories and the universal measurement of temperatures in ecological studies. For physiologists in particular, the thermometer, which first evolved as an instrument from a gadget of Galileo, is an indispensable tool; and the authors of this book have chosen to summarize that segment of temperature studies belonging to the realm of comparative physiology.

Those scientists who would reconstruct the past history of living things reckon temperature suitability as a prime condition for the origin and the continuance of life. Those who experiment with any living species ascertain the limitations and conditions imposed upon it by temperature before they go about whatever business they have with it. This fact is shown by the more frequent use of thermostats, incubators, and other constant-temperature equipment in the laboratory than any other one kind of control.

But if anyone supposes that temperature relations of organisms are basically understood, he will be disillusioned by this monograph. He will find instead that the influences of temperature upon organisms are not predictable except in a few respects, and that empirical knowledge is the basis of present analyses. Every species has to be subjected to a variety of tests before the rules of its responses can be known. But at least the tests needed are now recognizable. On a biochemical basis this empirical requirement may be anticipated for years to come, since the number of simultaneous reaction systems in any living unit numbers in the hundreds.

Each section of the present volume was written by a different author. The sections deal with (1) Poikilothermic Animals and Plants, (2) Microorganisms, and (3) Warm-Blooded Animals. Emphasis on the homeotherms is justified by the more extensive study they have received. The three authors have adopted a common format, with detailed subdivisions of subject materials. Together they cover a larger variety of temperature relations than has been comprehended in any previous work. Even so, completeness should not be expected. Documentation is substantial in 182 graphs, nearly 2000 references, tables, notes, and a thorough

index. Considerable emphasis is given to general concepts; sections containing them are clearly separated from those devoted to amassing data.

Chief emphasis falls upon the physico-chemical rules discernible in temperature influences. These rules are more than algebraic expressions for temperature coefficients; for much is known about enzymic actions, kinetics of processes, and lethal effects under the influence of constant temperatures. The work described is not limited, however, to effects of temperature; it also analyses regulations as manifested by subjection of organisms to a range of temperatures. Such regulations are especially well-known for a few warm-blooded animals and particularly for man.

The most outstanding contributions of the authors are their presentations of: (1) patterns of adaptation in oxygen consumption in relation to temperature for a wide variety of organisms; (2) physiological adaptations or acclimatizations in numerous plants, microorganisms, and animals; (3) factors determining the temperature extremes that organisms can endure; (4) analysis of resistance to heat and to cold in organisms, tissues, cells, spores, and thermophiles; (5) temperature optima and their relations to industrial productivities, disinfection, and the like; (6) sensory physiology and its relation to behaviors and regulations; and (7) manifestations of regulations and their analogies to some concepts of automation.

I think no one can view this panorama of temperature studies without glimpsing the general nature of certain temperature effects. Phenomena of resistance, adaptation, and enzymic relations belong to all the organisms studied. Mammalian physiologists and microbial physiologists need not rediscover one another's concepts if they read this summary carefully. Economy of effort may thus be achieved; and, of even more importance, new concepts applying to a wider variety of organisms may arise. If so, this volume will have served a high purpose.

E. F. ADOLPH

THE WATER RELATIONS OF TERRESTRIAL ARTHROPODS. *Camb. Monogr. exp. Biol., No. 5.*

By E. B. Edney. Cambridge University Press, New York. $3.00. 109 pp.; ill. 1957.

From the University College of Rhodesia and Nyasaland comes this critical review of more than two hundred research papers dealing with the acute problems of terrestrial arthropods in water economy. The internal regulation of water reserves and of electrolytes, as well as modern understanding of the physiology of excretion and osmoregulation, have been investigated. Rough correlations are noted between the presence and extent of cuticular wax and the ecological situations in which the animals live. The "saturation deficit" law is found to be theoretically unsound, but no simple replacement has been offered. Mechanisms for water-uptake are balanced against the sources of water-loss. The importance of the cooling effect of evaporation receives careful consideration, as does the hazard presented by ice crystals for terrestrial arthropods in cooler climates.

LORUS J. & MARGERY MILNE

THE PHYSIOLOGY OF FISHES. *Volume I, Metabolism. Edited by Margaret E. Brown. Academic Press, New York.* $12.00. xiii + 447 pp.; ill. 1957.

The nine collaborators for this volume (Barrington, Brown, Carter, Love, Mott, and Smith from the United Kingdom; Fry and Hoar from Canada; and Van Oosten from the U.S.A) have provided nine well-documented chapters, each with an up-to-date bibliography. The topics covered include respiration, the cardiovascular system, the gut and digestion, excretion and osmoregulation, the body covering, hormones, the gonads and reproduction, development and growth, and biochemical composition. Author and subject indexes weld the whole together. Coordination, receptors, effectors, and physiological genetics have been left to Volume 2.

"Although intended primarily for those interested in fishes and fishery research, this book is also written for general zoologists and comparative physiologists." A great deal that would interest a sports fisherman as well, such as the relation between growth rate and the size of neighboring fish, and the problems of fish which migrate between marine situations and fresh water, is partly concealed by technical language. General zoologists may be surprised at the range of viviparity and delighted with Van Oosten's account of the functions of the skin and scales—particularly the roles played by mucus. Carter's short chapter on air-breathing fish complements well the methodical presentation by Fry on aquatic respiration.

The Physiology of Fishes will be useful as a reference volume for many years. In view of its high price, one is tempted to speculate that longer accounts might have made the whole readable to sports fishermen, in which case a vastly larger market for the volume would have enabled the publishers to drop the price until the book would be widely attractive to scientists for their personal libraries.

LORUS J. & MARGERY MILNE

FIFTH ANNUAL REPORT ON STRESS *1955–56.*

Edited by Hans Selye and Gunnar Heuser; 17 contributors. MD Publications, New York (Medical Encyclopedia, New York). $20.00. 815 pp.; ill. 1956.

In order to read this volume intelligently, it will be necessary to learn what amounts, in many respects, to a new language. New and quite restricted meanings for familiar words are used throughout. Further, a new vocabulary including such terms as "A-CC phenomenon," " $\Delta^{1,4}$ corticoids," "eP," "eI," "homeokinetogenisis," "ponas," and "Ste-Rhi" must be learnt. A glossary of 107 such terms is provided. Of these, 55 are alphabetical abbreviations of non-familiar terms. Though I work in the field myself, I admit to having recognized on sight only 16 of the 107. I also grew a bit weary with explanations for the substitution of TTH for TSH (so that the latter may be reserved to mean "total nonprotein sulfhydryl"), with AGF and AWF (both meaning the same thing), with the abbreviation of cortisone to CON, and particularly with Ste-Rhi.

There are nine special articles in the volume. The one by Ingle is highly recommended, and those by U. S. von Euler, Scharrer, and Nelson will be of great interest to endocrinologists. All of the special articles are written in ordinary English medical terminology.

This book also contains 330 pages of annotated subject index plus seven pages of sorely-needed directions for its use. (The index makes free use of arrows which may point in any one of four directions. The arrows mean the same thing, but point in opposite directions if the subject under consideration appears as a chapter heading in *this* volume.) Actually, the subject index adds little to the 1953 and 1954 volumes of *The Quarterly Review of Medical Literature.*

The general index at the end of the book is also complicated by free use of arrows. In this case the arrows point in only one of two directions, and their meaning is not related to chapter headings.

The authors complain (p. 765) of the use of poor grammar by others, yet the following construction appears on page 36 of their own book: "... the definition does not postulate that neither the hypophysis nor the adrenal cortex are [*sic*] indispensable for the manifestations of all stress reactions." Further examples of such awkward and ungrammatical constructions will be frequently encountered. They tend to prolong reading time.

Each entry in the 201-page bibliography of this volume has been given a number with an alphabetical prefix to facilitate its location by anyone who goes to Montreal.

J. W. Woods

Aspects du Métabolisme des Stéroïdes Hormonaux. *Actualités Biochimiques No. 19.*

By Gregory Pincus. Masson & Cie., Paris; Édition. Desoer, Liège. 1,000 fr. (paper). iv + 108 + ii pp.; ill. 1955.

This monograph contains six edited lectures given by G. Pincus during a term as visiting professor at the College of France. In French, as in English, the experiments described and the presentation of the data conform to the high standards we have come to expect from the Worcester group, and from Pincus in particular.

In this course of lectures, the author covers the biosynthesis and synthesis *in vitro* of adrenal steroids, corticosteroidigenesis in man, biosynthesis of gonadal hormones, the metabolism of steroids with particular reference to those of gonadal origin, and finally, steroid metabolism from a geriatric point of view. There is a short and intriguing postscript in which he discusses parthenogenesis in the rabbit. For the most part, however, any reader who is familiar with the English literature will find little that is new in this monograph.

J. W. Woods

Les Stéroïdes Urinaires. *Étude Biologique et Clinique au Cours de la Gestation Normale et Pathologique.*

Masson & Cie., Paris. 650 fr. (paper). iv + 131 pp.; ill. 1954.

The papers reproduced in this monograph were given during a colloquium on luteal function held in Paris three years ago. All seven papers are by clinicians, and all of the data presented is from clinical material. Each of the seven articles deals with some phase of urinary steroid excretion during gestation. The data presented, with rather elegant statistical treatment in some cases, were obtained from a large number of patients undergoing normal or pathological pregnancies. The cases described will probably be of interest to obstetricians, to gynecologists, and perhaps to clinical endocrinologists. Clinical and laboratory investigators who are familiar with the English language literature will have seen these or similiar data previously.

J. W. Woods

ANIMAL NUTRITION

Advances in Food Research. *Volume VII.*

Edited by E. M. Mrak and G. F. Stewart. Academic Press, New York. $9.50. x + 404 pp.; ill. 1957.

Seven articles of very varied nature make up this seventh volume of the series. The Profile Method of Flavor Analysis, by J. F. Caul, plunges the biologist into a familiar dilemma—"no known mechanical or physical devices can do the combined work of the human mouth, nose, and brain in detecting and evaluating flavor." The profile method advocated by the author is essentially that of a well-organized differential diagnosis, with subjective ratings for each signifi-

cant component—a method believed to give more consistent and understandable results than others. Standardized conditions are recommended for testing, especially where perception changes with time. The Japanese fishing industry is represented by a paper, under the joint authorship of Y. Tomiyasu and B. Zenitani, entitled Spoilage of Fish and its Preservation by Chemical Agents. In common with numerous olfactory and gustatory agents, the chemical culprits in the "very ancient and fish-like smell" are being rapidly finger-printed, and their antecedents established. The origin and identification of various amines, ammonia, and volatile fatty acids are discussed in some detail, as well as the nature of the much-to-be-avoided green spot in swordfish. The post-mortem decrease in electric resistance offers an intriguing possibility that time since death may be determined. The preservative efficacy of chlorine-liberating compounds, benzoic acid, other acids and brine, sodium nitrite, and antibiotics are also reviewed. The third article, by W. J. Scott, on Water Relations of Food Spoilage Microorganisms, is an excellent example of precise physical approach to a biological problem. In a preliminary succinct review, the author establishes the importance of the property termed "water activity," which is simply the ratio of the vapor pressure of the solution to that of the solvent. In the remainder of the article he spells out the methods by which water requirements of microorganisms are studied; the factors affecting the water requirements; the special cases of halophilic, osmophilic, and xerophilic organisms; applications to food preservation; and certain research problems.

Chlorine in Food Plant Sanitation, by W. A. Mercer and I. I. Somers, probably holds less of interest for biologists than the other articles. Freeze Drying of Food Products, by J. C. Harper and A. L. Tappel, deals with a very important applied problem, in connection with which biophysical problems of a wider interest are discussed. The fundamental difficulty is one of transferring heat through food material in such a way that rapid evaporation is secured, without melting of the as yet unevaporated ice and without undue warming of the portions already dried. The relative advantages of conductive, radiant, and dielectric heating are discussed. A secondary problem concerns the removal of water vapor from the evaporative area. Those interested in specific foods will find 28 pages devoted to them. B. Idson and E. Braswell have furnished an article which thoroughly reviews the complicated chemistry, physical chemistry, and technology of gelatin. The reader cannot long doubt that "gelatin actually is a collective name covering a wide range of materials." It would appear that the art of gelatin manufacture still has to find full explanation in physical and chemical terms. A series of idealized drawings on scales ranging from 20 μ to 200 Å suggests that the inherent structure yields to subdivision right down to the molecular level. The relative importance of covalent, electrostatic, and hydrogen bonds in holding the structure together is discussed. Glycine accounts for about one-third, and cyclic amino acids together with proline and hydroxyproline for another third, of the molecular structure. There is a wide spread in molecular weights, from less than 10,000 to 180,000, with a mode in the 20,000 to 40,000 class. Sol-gel relationships are discussed in some detail. Some interesting facts are that 100 million pounds of gelatin are produced annually, that half this amount comes from the United States, that 65% goes into desserts, and that "a marshmallow is a colloidal dispersion of a gas within a liquid." A concluding article by C. Nieman on Licorice will no doubt leave some readers with fond memories of a weighty meal well-digested, although, as the author points out, this flavoring agent is more commonly used in tobacco than in food in the United States.

DOUGLAS H. K. LEE

LES VITAMINES. *Biochimie, Biologie, Emploi Thérapeutique.*

By Henri Thiers. Masson & Cie., Paris. 4,600 fr. (cloth); 4,000 fr. (paper). iv + 626 pp.; ill. 1956.

This general discussion of the biological and biochemical aspects of vitaminology is pointed towards the use of the vitamins in therapy as well as in the maintenance of nutritional equilibrium. It is compiled from information gathered from a number of more detailed sources, and is presumably for the use of many French students of medicine.

It is not intended to meet the requirements of a research reference work and does not do so. It lacks even the bibliography which could have extended the usefulness of the present form of the book.

R. G. GRENELL

SYMPOSIUM ON THE ROLE OF SOME OF THE NEWER VITAMINS IN HUMAN METABOLISM AND NUTRITION. *Proceedings of the Nutrition Symposium held at Vanderbilt University School of Medicine, Nashville, Tennessee, October 20–21, 1955. Nutrition Symposium Series, Number 12.*

28 Contributors. The National Vitamin Foundation, New York. $2.50 (paper). 137 pp.; ill. 1956.

Vitamin B_6 and vitamin E are the main topics of discussion of this symposium, with one paper devoted to pantothenic acid metabolism and two chapters to vitamin B_{12} nutrition. All of the papers are presented by active workers in the vitamin field; yet they represent a wide spectrum of interests—including nutrition, metabolism, neuropathology, and others.

While the primary purpose of the symposium was a

discussion of the vitamins in human nutrition and metabolism, a considerable portion of the data presented concern the findings first made on experimental species. Those papers dealing primarily with human beings include: Abnormal Vitamin B_6 Metabolism in Pregnancy and Various Disease States; Metabolism of B_6; Tocopherol and Tocopherol Deficiency in Infants and Children; Alpha-tocohydroquinone and Muscular Dystrophy; Limited Tocopherol Intake in Man with Relationships to Erythrocyte Hemolysis and Lipid Oxidation; Pantothenic Acid Metabolism; Absorption of Vitamin B_{12}; and Vitamin B_{12} Serum Levels and Pregnancy.

Each of the papers presents current data and includes numerous references. The volume will certainly be of considerable interest to clinicians and research workers in nutrition and biochemistry.

R. VAN REEN

SYMPOSIUM ON VITAMIN METABOLISM. *Nutrition Symposium Series, Number 13. Proceedings of a Symposium held under the auspices of The University of Texas and The National Vitamin Foundation, March 6, 1956.*

9 Contributors. The National Vitamin Foundation, New York. $2.50 (paper). 118 pp.; ill. 1956.

The introduction to this symposium was given by S. Ochoa, who presented a brief summary of the enzymatic mechanisms involved in the conversion of some of the vitamins to their biologically active forms as coenzymes. Most of the papers are short, critical discussions of current work on the metabolism and functions of the active forms of the B-complex vitamins and of vitamin C. A more general review and historical background, as well as current data, are presented in the cases of niacin and vitamin B_6. Each paper is followed by current references and by further discussion of the work by another investigator in the field.

The papers presented are: The Metabolism of Thiamin and Lipoic Acid; The Biogenesis of Riboflavin; The Metabolism of Niacin; Metabolism of Vitamin B_6 and its Derivatives; The Metabolism of Pantothenic Acid; The Metabolism of Folic Acid and Folinic Acids; The Metabolism of L-Ascorbic Acid; and The Metabolism of Biotin.

R. VAN REEN

BIOPHYSICS AND GENERAL PHYSIOLOGY

ATOMIC ENERGY RESEARCH AT HARWELL.

By K. E. B. Jay. Philosophical Library, New York. $4.75. xxi + 144 pp. + 12 pl.; text ill. 1955.

At least the U. S. Atomic Energy Commission has a recognized Division of Biology and Medicine. To judge from this book, the Atomic Energy Authority of the United Kingdom has Production, Reactor, and Isotope Programmes; Physics, Chemistry and Chemical Engineering, and Metallurgy Divisions; and various subsidiary services. Nowhere, even in "Extra-mural Research," does biology enter the picture. The genetic and pathologic effects of nuclear radiation are kept carefully off-site.

P.S. The Appendix, on the last page, notes the existence of both a Health Physics Division and a Radiobiological Research Unit. Apparently they are not considered to have accomplished anything worth mentioning. Inasmuch as Great Britain is leading the world in the development of nuclear reactors for power production, and the population may in consequence incur a steadily increasing risk of exposure to nuclear radiations, one would have supposed more of the available funds and skilled personnel would be devoted to an analysis of the dangers and to discovery of some means of circumventing them.

BENTLEY GLASS

BIOCHEMISTRY

CURRENTS IN BIOCHEMICAL RESEARCH, 1956.

Edited by David E. Green. Interscience Publishers, New York and London. $10.00. xvi + 697 pp.; ill. 1956.

In his introduction to the twenty-seven essays which comprise this impressive book, David E. Green gives a thumbnail sketch of some of the more important changes and accomplishments of the past decade. The accelerated pace of progress in biochemical research has not yet subsided; it pulses through each contribution to this volume. The subject matter itself is an indication of things that are yet to come.

Currents in Biochemical Research does not suffer, as do so many symposia, the possibility of becoming outdated even before the printer's ink is dry. It is, rather, a milestone at which we may pause to reflect upon the years gone by.

The space devoted to each topic corresponds in some degree to the progress made in the concerned field of biochemistry since the last *Currents* was written. Eight chapters of the book are devoted to strictly enzymological aspects as elucidated by S. Spiegelman and A. M. Campbell (Enzyme Induction), Efraim Racker (Enzymes as Reagents), Henry R. Mahler (Enzyme Complexes), Hugo Theorell (Prosthetic Group, Coenzyme and Enzyme Interrelations), Britton Chance (Enzyme-Substrate Compounds and Electron Transfer), G. Robert Greenberg (Multiple Enzyme Systems), Robert A. Alberty (Enzyme Kinetics), and Frank M. Huennekens (Nucleotides and Coenzymes). The last

mentioned topic is covered from the nutritional point of view (Vitamins and Growth Factors) by Esmond E. Snell.

Other chapters also discuss enzymatically catalyzed reactions, but are differently oriented. The structure and biosynthesis of proteins, hormones, nucleic acids, and porphyrins are covered by Konrad Bloch, Barbara W. Low and John T. Edsall, Gregory Pincus, F. Sanger, Waldo E. Cohn, and David Shemin. The latest progress in our understanding of sugar interconversions in nature is outlined by Luis F. Leloir, and photosynthetic reactions and mechanisms are discussed by J. A. Bassham and M. Calvin.

Physiological biochemistry is represented by chapters on muscle contraction (Manuel F. Morales and Jean Botts), nerve activity (David Nachmansohn and Irwin B. Wilson), and blood (Douglas M. Surgenor). Hemoprotein reactions are covered in a separate chapter by Philip George.

Abnormal biochemical conditions are considered in chapters on disease (DeWitt Stetten, Jr.) and, more specifically, on carcinogenesis (Harold P. Rusch). One chapter on viral growth (A. D. Hershey) and one on Bacterial Fermentations (H. A. Barker) are also included.

Two chapters of this volume, one posing some basic biochemical questions (Fritz Lipmann) and one discussing cellular biochemistry (Carl F. Cori), indicate most clearly those fields of biochemistry the omission or brief mention of which in *Currents* is a significant comment on their present status of uncertainty. For example, Lipmann emphasizes our lack of understanding of mechanisms underlying the patternization in biochemical structures, a topic of paritcular importance to the biochemical geneticist; and Cori's chapter reveals, by implication, our insufficient comprehension of fundamentals underlying transport mechanisms that cross membranes of cells and cellular particles.

Topics and authors for *Currents in Biochemical Research* have been chosen with care, and the volume deserves a place on the shelf of every biochemist.

CLAUDE F. BAXTER

ADVANCES IN CARBOHYDRATE CHEMISTRY. *Volume 11. Edited by Melville L. Wolfrom; Associate Editor, R. Stuart Tipson. Academic Press, New York.* $11.00. xviii + 465 pp.; ill. 1956.

The high standard established in this series of publications is maintained in Volume 11, which provides an array of thorough and timely surveys on topics of interest to carbohydrate chemists, biochemists, and organic chemists in general. With eight articles covering a broad range of interests and written by authors from four different countries, the current volume continues also to sustain the international character of the earlier ones.

The first article, Periodate Oxidation of Carbohydrates, by J. M. Bobbitt, is a discussion on the application of periodate cleavage to carbohydrates. Periodate oxidation has proved to be the most powerful tool for the study of carbohydrate structure since the introduction of the methylation procedure by Irvine and Haworth during the first two decades of this century. The author illustrates many of the different types of oxidation and indicates their various applications. This article constitutes the most complete review of the subject since that writtee by E. L. Jackson in *Organic Reactions* in 1944.

The subject of The Osones is reviewed by S. Bayne and J. A. Fewster. Although considerable information has been accumulated on this subject since Emil Fischer prepared osones nearly seventy years ago, this is the first modern comprehensive review on the chemistry of these compounds.

Under the topic, Reactions of Monosaccharides with Beta-Ketonic Esters and Related Substances, F. G. González treats the known reactions between reducing sugars and β-ketonic esters. He gives detailed procedures for the preparation of the condensation products and tables describing their properties. The author is also concerned with the possible biological significance of these compounds in the animal body.

A thorough discussion of the structure, biosynthesis, and physical and chemical properties of Kojic Acid is presented by A. Beĉlik. Kojic acid (5-hydroxy-2-(hydroxymethyl)-4H-pyran-4-one) is of particular biological interest because its formation is the simplest known case of the biological conversion of a sugar to a γ-pyrone. A knowledge of the mechanism of its formation may lead to an understanding of the biological synthesis of such complex γ-pyrone derivatives as flavones, flavonols, and furochromones, which are abundant in plants.

L. Hough and J. K. N. Jones are concerned with the complex subject of Biosynthesis of the Monosaccharides in nature. These authors discuss a multitude of enzymatic reactions and the resulting intermediate compounds involved in processes leading to the formation of various monosaccharides. The formulas of some forty monosaccharides known to exist in nature are listed in a table.

The chemistry of Branched-Chain Sugars of Natural Occurrence is summarized by F. Shafizadeh. This author points out that relatively few branched-chain sugars are known to occur in nature. Prior to the study of the structure of the antibiotic streptomycin, the only natural products which were known to contain a branched-chain sugar were flavone glycosides of the parsley plant and the hamameli-tannin from the bark of the witch hazel. With the recent discovery of the existence of several other branched-chain sugars as

constituents of certain bacterial polysaccharides and of antibiotic substances, the branched-chain sugars are assuming greater significance.

A comprehensive review of the biological important group of Nucleic Acids is presented by G. R. Barker. The last chapter, Aspects of Physical Chemistry of Starch, by C. T. Greenwood, is a survey of the results of physical measurements of starch and of a number of other polysaccharides.

The volume contains an obituary of the late Kurt H. Meyer written by R. W. Jeanloz. Meyer was a noted chemist who made significant contributions to knowledge of the structure of cellulose and starch. Also included is a Cumulative Index to Volumes 1–10, which will afford the reader a ready access to the information contained in the entire series.

W. Z. Hassid

Polysaccharides in Biology. *Transactions of the First Conference, April 27, 28, and 29, 1955, Princeton, N. J.*

Edited by George F. Springer. Josiah Macy, Jr. Foundation, New York. $5.00. 271 pp.; ill. 1956. This volume is a record of the transactions of a conference centered around four main papers presented in an informal manner. The first paper, Problems of Communication: Nomenclature, by M. L. Wolfrom, is a consideration of nomenclaturial problems of the great multitude of carbohydrates and their derivatives. In discussing the rules adopted within the last decade by the Carbohydrate Nomenclature Committee of the American Chemical Society in cooperation with the British group of the Chemical Society, this author emphasizes the "need of a rational system, so that given the name, the formula can be written, and given the formula, the name can be written." The lack of a more precise nomenclature for carbohydrates is pointed out by examples such as this: "The biochemists call D-*erythro*-pentulose ribulose and they call D-*threo*-pentulose, xylulose. However, since the centers are two, the prefix D-*erythro* should be employed. There is not a third center in here, so it should not be named from the pentose D-ribose. The correct name for it is D-*erythro*-pentulose."

In the article Problems of Classification, Karl Meyer is concerned with nitrogen-containing polysaccharides for which there has been no established nomenclature. These polysaccharides are considered under the general groups mucopolysaccharides, mucoproteins, mucoids, and glycoproteins. The polysaccharides of the first three groups contain hexosamine as an essential component. Those of the fourth, glycoproteins, contain comparatively little hexosamine, and sometimes are entirely devoid of it.

The discussion of Bacterial Polysaccharides, by Michael Heidelberger, is limited primarily to immunologically specific polysaccharides, in which subject the author was a pioneer who contributed more than any other worker in that field. Heidelberger questions the existence of non-immunological polysaccharides. His recent work has shown that practically any polysaccharide is potentially immunologically specific, if antibodies of suitable configuration are present to react with it.

The last chapter, Blood Group Substances, by W. T. J. Morgan, is a discussion of the chemical basis of specificity of the human blood group characters. The author begins with an account of the biological aspects of the subject by reviewing the original experiments of Karl Landsteiner and earlier observations of geneticists concerning the different blood group characters in families. He then proceeds with an account of the isolation, purification, and characterization of the materials which are responsible for the characteristic serological behavior of the erythrocytes, tissue fluids, and secretions.

The high quality of the reports, and the extensiveness of the informal discussions, makes this volume an interesting and useful addition to the biochemical literature.

W. Z. Hassid

Biochemistry of Nitrogen. *A Collection of Papers on Biochemistry of Nitrogen and Related Subjects dedicated to Artturi Ilmari Virtanen on the Occasion of his 60th Birthday, January 15, 1955. Annales Academiæ Scientiarum Fennicæ, Series A. II. Chemica, 60.*

Edited by B. J. Myrberg. Suomalainen Tiedeakatemia, Helsinki. 2300 Fmk. (paper). ii + 535 pp. + 2 pl.; text ill. 1955.

These papers, some fifty in number, range from such topics as Studies on Magnesium Diabetes, by P. Suomalainen, through C. N. Hinshelwood's Mutations and Adaptations in Bacteria, to Linus Pauling's The Energy Change in Organic Rearrangements and the Electronegativity Scale. A sizable spectrum of biochemistry and related areas is covered by the various papers, with the field of nitrogen metabolism most heavily represented. The latter includes Nitrogen Fixation by *Aerobacter aerogenes*, by P. B. Hamilton and P. W. Wilson; The pN_2 and the pO_2 Function for Nitrogen Fixation by Excised Soybean Nodules, by R. H. Burris, W. E. Magee, and M. K. Bach; Hydroxylamine Reductose, by S. Taniguchi, H. Mitsui, K. Nakamura, and F. Egami; The Oxidation of Amino Acids by Plant Mitochondria, by N. Rautanen and J. M. Tager; Chromatographic Experiments with Proteins,

by A. Teselius; Recent Advances in the Chemistry of Some Natural Polymers Containing Amino Sugars, by M. Stacey; and Some Observations on the Nitrogen Fixing Bacteria of the Genus *Beijerinckia* Derx, by A. J. Kluyver and J. H. Becking.

An article by A. R. Todd, The Synthesis of Nucleotide Coenzymes, and one by E. Chargaff, Remarks on the Physiological Importance of the Nucleoside Phosphotransferases, cover some phases of nucleoside interest. The heme protein area is treated in R. Lemberg's Studies on the Prosthetic Group of Cytochrome Oxidase and Cytochrome *a*, in G. Hevesy's and R. Bonnichsen's Some Aspects on the Effect of Irradiation with Roentgen Rays on Hemoglobin Formation, and in H. Theorell's and Å. Åkeson's Reversible Splitting of Homogeneous Horse Myoglobin. Other papers include Bacterial Formation of Adenosine-Properties of the Cell-free Enzyme System in *E. coli*, by J. L. Ott and C. H. Werkman; Activity pH Curve of Yeast Convertase and the Mechanism of Hydrolase Action, by K. Myrbäck; The Fate of Uniformly Labelled C^{14} Fructose in the Isolated Rat Diaphragm and Rat Brain and Liver Slices, by A. Beloff-Chain, R. Catanzaro, E. B. Chain, I. Masi, and F. Pocchiari; Zum biologischen Abbau der Essigsäure. VII. Die Synthese von Citronensäure durch gefrorene Hefe, by F. Lynen and H. W. Kalb; and Arsenolysis and Phosphorolysis of Citrulline, by H. A. Krebs and L. V. Eggleston.

Forty of the papers are in English, the remainder in German or French. The volume reflects a growing tendency to dedicate the entire contents of a single issue to an outstanding personality in biochemistry. It is valuable for its compilation of a series of interesting and diverse papers between the covers of a single publication. On the other hand, some of the work presented is merely a duplication of results and discussions already given elsewhere in the literature. Unfortunately, the volume has a paper cover and lacks both subject and author indexes.

ALVIN NASON

BIOCHEMICAL INDIVIDUALITY. *The Basis for the Genetotrophic Concept.*

By Roger J. Williams. John Wiley & Sons, New York. $5.75. xiii + 214 pp.; ill. 1956.

R. J. Williams, one of our most productive, experienced, and widely known biochemists, is President of the American Chemical Society this year. He has chosen here to champion the importance, in a particular direction, of an age-old problem—biological variability. It is Williams' major thesis that, keeping in mind the "infinite variety of interplaying genetic factors," the insights and implications associated with hereditary factors in morphology and disease can and must be profitably employed in the examination and interpretation of the metabolic processes of the total organism. It is stated that every individual organism having a distinctive genetic background has distinctive nutritional needs which must be met for optimal well-being. From this it follows that an understanding of the individual's unique heredity may aid in properly treating his unique environmental needs. The author stresses particularly the "need in human biology and medicine for more attention to variability and individuality at the physiological and biochemical levels." The immediate problem which arises from such considerations, of course, is the perennial, ubiquitous one of the real meaning of normality. A vast number of implications obscure a knowledge of the "normal" differences between "normal" individuals. Such knowledge most certainly is lacking in the most important areas of its medical application. For this reason alone, Williams' book should be called to the attention of investigators and practitioners of medicine, despite the need for more data to support the author's particular thesis and the questionable nature of some of his "facts."

That a discussion such as this book attempts must extend into many areas will be obvious. The very interesting implications for psychiatry stress the degree of importance to be placed on hereditary factors. There is no doubt in my mind, at least, that R. J. Williams has performed his greatest service by confronting us with the need for looking squarely at a basic problem which is too often neglected.

R. G. GRENELL

MICROBIOLOGY

THE MICROBIAL WORLD.

By Roger Y. Stanier, Michael Doudoroff, Edward A. Adelberg. Prentice-Hall, Englewood Cliffs. $8.00. xxii + 682 pp.; ill. 1957.

This book is "an attempt to present a modern synthesis of microbiological knowledge in a form intelligible to the beginner" (*cf.* Preface). There are three main parts: I, on the properties of microörganisms; II, (which includes the medical portion) on the ecology of microorganisms; and III, a general background exposition of basic biological principles. That the material is up to date and is well and clearly described proves that to be scientifically accurate a book need not be murky or pedantic. I noticed no errors of fact or of interpretation. The figures and tables are abundant and excellent.

At the same time, it is probable that students who do not have a good background in biology, in organic and inorganic chemistry, as well as in physics, will find the book difficult to assimilate. Part III, although splendidly presented, will probably not compensate for

a lack of previous grounding in general biology. Furthermore, the index is weak—*p*-aminobenzoic acid receives an entry, but *p*-aminosalicylic acid (mentioned in connection with tuberculosis, p. 517) does not. This weakness in indexing limits the usefulness of the book as a reference text. Nevertheless, no textbook on microbiology (or any subject) is outstanding in all respects. As a general reading presentation for well-prepared students, the book is among the best of those currently available and can be highly recommended on that basis.

WALTER C. TOBIE

FUNDAMENTALS OF MICROBIOLOGY. *Second edition, illustrated.*

By Martin Frobisher. W. B. Saunders Company, Philadelphia and London. $6.50. xxii + 617 pp.; ill. 1957.

When the fourth edition of this book was reviewed (*Q.R.B.*, 26: 96. 1951), it was suggested that its title be changed from "Fundamentals of Bacteriology" (as it was then called) to "Fundamentals of Microbiology." This change has been made—though the reviewer takes no credit for it—and the new title indicates the scope of the book much more accurately. As before, both general principles and special topics receive excellent treatment. Several portions of the text have been completely revised and the subject matter and references bring the material to the year 1956.

Since the book is written for students having some previous background in chemistry, physics, and biology in general, a variegated and intelligent approach is possible. Many beginning texts assume not only that the students have no knowledge of microbiology, but also that they are half-stunned semi-literates having no previous knowledge of *any* science. Such an approach may be necessary where ill-prepared individuals are allowed to study microbiology. Institutions where such policies are in effect will find this book too much for them. In places where the neophytes in microbiology are better prepared in the basic sciences, the book will be of extreme value and usefulness. On such a basis, I recommend the book most heartily.

WALTER C. TOBIE

AN OUTLINE OF BACTERIOLOGY AND IMMUNITY.

By Ronald Hare. Longmans, Green & Company, London, New York, Toronto. $7.00. ix + 418 pp.; ill. 1957.

This book "is based on the course of lectures given to clinical students at St. Thomas's Hospital" in London. According to a résumé on the back of the jacket, "Viruses and fungi are given weight equal to that accorded to the bacteria," while "the fundamental emphasis is laid rather on the fundamental principles involved in the relationship between microörganisms and man than on the minutiae of bacteriological technique or the cultural and other characteristics of microbes." In my opinion, these extracts characterize the book rather well. It seems to be well and clearly written, and I noticed no errors. At the same time the book seems to be of very limited scope as a medical text, perhaps because it has been overcondensed to meet the particular requirements of a particular teaching institution. Whether it would be of equal value in other schools is debatable. Practically all of the material on the pneumococcus *Klebsiella pneumoniae* is condensed into about a page and a quarter (on pp. 322–323), although some other organisms, such as *Mycobacterium tuberculosis*, receive more adequate treatment. Yet since the book is presented as an outline text only, perhaps we should accept it as such. Those who are interested in such an outline should examine the work in the original to see how well it may meet their requirements.

WALTER C. TOBIE

PRÉCIS DE BACTÉRIOLOGIE MÉDICALE. *Deuxième Édition.*

By Pierre Gastinell; five collaborators. Masson et Cie., Paris. 6,000 fr. (paper); 6,700 fr. (cloth). vii + 1243 pp. + 1 pl.; text ill. 1957.

This sizeable book contains a very large amount of information presented in a moderately advanced manner. In fact, so much material is included that many of the topics touched upon, such as antibiotics and antibacterial synthetic drugs, are treated very superficially. In the purely laboratory aspects of medical bacteriology, however, the treatment is comprehensive and exhaustive. Pathogenic microorganisms other than bacteria are also considered, although treatment of macroparasites is omitted from this edition (1st edition: *Q.R.B.*, 25: 112. 1950). There are abundant references, an adequate index, and an absence of errors of fact or interpretation. The general "feel" of the text is that of a French equivalent to the Parke and Williams of thirty years ago. The work is thoroughly creditable in its field, but offers little of outstanding interest to American microbiologists other than an opportunity to read a French point of view on various topics.

WALTER C. TOBIE

LES BACTÉRIES LYSOGÈNES ET LA NOTION DE PROVIRUS. *Monographies de l'Institut Pasteur.*

By François Jacob; preface by André Lwoff. Masson & Cie., Paris. 800 fr. (paper). viii + 176 pp. + 1 pl.; text ill. 1954.

The last decade has witnessed the integration of virology with genetics—a major achievement in biology. Central to this achievement is the operational concept of "provirus," that is, the hereditary ability of a cell to generate a virus. In bacteria, the identification of some proviruses with genetic elements that can be located within the linear linkage map of the hereditary factors of the cell has given the provirus a material reality and has indicated that the details of genetic specificity of a virus are coded in the same chemical language as those of all other genetic factors. Jacob's monograph summarizes lucidly the basic knowledge of lysogeny, or the condition of potential virus production in bacteria, and describes in detail the remarkable original work of the author up to 1954. Even by itself, this work would represent an impressive contribution. It includes studies on the induction of virus production from provirus in the lysogenic cells; on the biosynthesis of the virus; on the genetic determinants of the lysogenic condition, both in the host cell and in the provirus itself; on defective proviruses; on bacteriocins, antibiotic substances produced by bacteria under conditions similar to activation of proviruses; and several others. Since current progress in this field is remarkably rapid and since the author has played a major role in this progress, the monograph assumes added interest in that the many original ideas expressed, which were just being formulated at the time of writing, have now been brought to fruition and can be appreciated.

S. E. Luria

The Nitrogen Metabolism of Micro-Organisms. *Methuen's Monographs on Biochemical Subjects.*

By B. A. Fry. John Wiley & Sons, New York; Methuen & Company, London. 9s. 6d. ix + 166 pp. + 3 pl.; text ill. 1955.

This book is the seventh in the series of Methuen's monographs on biochemical subjects. It is a small volume that fulfills its primary aim in providing a compact and more or less up-to-date review of the current status of nitrogen metabolism in microorganisms. The book is apparently based on a series of lectures given in a microbiology course at the University of Sheffield. Fry has very admirably encompassed a wealth of succinct facts in this small monograph. His approach has been to analyze the component steps of the all-important biological nitrogen cycle with respect to the biochemistry of the reactions and the microorganisms involved. Some emphasis has been accorded the synthetic mechanisms, such as proteins, and the metabolic role of nucleic acids. The introductory chapter very neatly includes discussions of energetics of biological systems and general aspects of nutrition. This is followed by chapters on amino acid catabolism, nitrification and denitrification (including the reduction of nitrate and nitrite to ammonia), nitrogen fixation, amino acid synthesis, amino acid absorption, peptides and proteins, proteolytic enzymes, nucleotides and nucleic acids, and chemotherapeutic agents.

This small volume is an excellent addition to the Methuen Series. It compares, in many respects, with some of the better reviews in the field. Remarkably good coverage and organization for a book of its size and scope make it a valuable contribution for teacher and student in the area of nitrogen metabolism. Yet it is unfortunate that the editors did not see fit to include an author index.

Alvin Nason

Biological Treatment of Sewage and Industrial Wastes. *Volume I. Aerobic Oxidation.*

Edited by Brother Joseph McCabe, F.S.C., and W. W. Eckenfelder, Jr. Reinhold Publishing Corporation, New York. $10.00. vii + 393 pp.; ill. 1956.

This is the edited collection of papers on principles and methods of aerobic waste treatment presented by more than thirty specialists during a three-day symposium at Manhattan College in the late spring of 1955. A significant departure from current group discussions waste treatment has been made here in that principles, rather than technology, of industrial waste treatment have been stressed. It is the first of a series of such specialized basic reviews of waste engineering organized by the Manhattan College workers.

Discussions of special interest to biologists are presented in the first group of ten papers on the applied bacteriology and physiology of surface films and flocs, and on the application of fermentation-rate values to waste treatment and to stream-loading design. The feature of these treatments that should interest bacteriologists and biochemists is the transfer of a few simple principles of fermentation to large, widely varying engineering processes. The bacteriological background is primitive, but it is necessary to understand the scale and economics of waste disposal to realize why it has been developed to such a limited degree.

The larger fraction of the papers deals with the activated sludge process, presently gaining popularity in the treatment of industrial wastes. There is, in consequence, an extended and valuable discussion of the physical and engineering principles of aeration and oxygen-transfer in tank systems.

Biologists currently working in the field of stream sanitation and in industrial waste research, especially, will want this book as a specialized reference. The papers were prepared for conference presentation and have

not been published in the professional journals. They include useful personal observations of active workers. Each of the four sections of the symposium is followed by a bibliography, and there is a well developed subject index.

CHARLES E. RENN

DISPOSAL OF SEWAGE AND OTHER WATER-BORNE WASTES. *Based on a translation of* Taschenbuch der Stadtentwaesserung, *16th Edition (1956), by Karl Imhoff.*

By Karl Imhoff, W. J. Müller, and D. K. B. Thistlethwayte. Butterworths Scientific Publications, London. 45s. ix + 347 pp.; ill. 1956.

This is a practical, descriptive manual of waste disposal engineering. In America, it fits the requirements of public health officers and engineers who are concerned primarily with the review and general supervision of waste disposal operations.

The individual problems of sanitary waste disposal are described, the principles to be applied are indicated, and the dimensions of practical design are given for each case. The conditions under which a treatment technique is adaptable and the common causes of failure are given. Although most of the experience cited arises from work with the stronger wastes of the Continent and of England, departures respected in American practice are carefully treated.

A very serious limitation to much of our professional literature in sanitary engineering is that difficulties with treatment processes and failures are rarely reported. This handbook, which includes much from Dr. Imhoff's extensive personal experience, examines processes more critically. Research workers in waste disposal should use it as a guide in fitting treatment to community needs. The book is also well adapted to serve as an introductory reference in undergraduate sanitary engineering courses, though most sanitary engineering departments in the U. S. A. will require supplementary design texts to satisfy engineering training requirements. Complete bibliographies appear at the end of each chapter. British and German references and a detailed subject index are added values.

CHARLES E. RENN

HEALTH AND DISEASE

ERGEBNISSE DER MEDIZINISCHEN GRUNDLAGENFORSCHUNG.

Edited by K. Frk. Bauer, with the help of K. Bucher, A. Grumbach, A. Kornmüller, J. Külnau, H. Schaefer, and H. Schoen. Georg Thieme Verlag, Stuttgart; [Intercontinental Medical Book Corporation, New York.] DM 129. viii + 855 pp.; ill. 1956.

Under the editorial direction of Bauer of Erlangen, nineteen comprehensive essays on currently active areas of research fundamental to medicine are presented here. All are in German, although contributing authorities include scientists in Chicago, in Manchester (Eng.), and in Nancy. The topics covered are: (1) The Structure of the Bacterial Surface Membrane and Capsule, (2) Skin Tuberculosis, (3) Mitochondria, (4) The Fine Structure of the Nucleus and Cytoplasm in Relation to Cell Function, (5) Antimetabolites, (6) The Kinetics and Thermodynamics of Enzyme Reactions in Living Cells and Tissues, (7) Vitamins, (8) Basic Processes of Muscular Contraction, (9) The Essential Amino Acids, (10) Therapy Directed at Tissue Function, e.g., radioactive iodine, thiourea derivatives, etc., (11) Tissue Transplantation, Therapeutic Use of Tissue Extracts (e.g. Bogomoletz serum), etc., (12) Allergy, (13) The Biophysics of Radiation, (14) Hypothermia, (15) Neurohistology, (16) Embryology of the Human Cerebral Cortex, (17) Function of the Pituitary, (18) Embryology in the Study of Disease, and (19) Dimensions in the Morphology of Man. The essays are authoritative and are recommended without reservation to workers in each of the fields covered.

VICTOR A. MCKUSICK

ANALYTICAL PATHOLOGY. *Treatises in the Perspective of Biology, Chemistry, and Physics.*

Edited by Robert C. Mellors; foreword by Eugene L. Opie. McGraw-Hill Book Company, New York. $12.00. xii + 477 pp.; ill. 1957.

Under the editorship of a pathologist at New York's Sloan-Kettering Memorial Hospital and Cornell's Medical Center, and with a foreword by the venerable pathologist, Eugene L. Opie, eight monographs are presented in this volume. They interpret *pathology* in its most literal sense— "the study of disease"—without the restrictive frame-of-reference of gross and microscopic morphology. Furthermore, as indicated by the title, the perspective in which the several domains are viewed includes biology, chemistry, and physics—disciplines which are continually contributing to the medical research laboratory and, indeed, to bedside care.

The topics considered are: Cancer, by Mellors; Arteriosclerosis and Hypertension, by John W. Gofman; Inflammatory and Vascular Disease of the Renal Glomerulus, by David B. Jones; Cholemia, Ascites and Hemorrhagic Phenomena in Hepatic Failure, by Oscar D. Ratnoff; The Adenohypophysis, by Agnes Burt Russfield; Macrocytic Anemias, by John F. Mueller; Abnormal Hemoglobins, by John J. Neill; The Role of

Connective Tissue in Hypersensitivity, by Bernard M. Wagner.

Four of the eight authors are not pathologists in the conventional sense. This fact reflects the wholesome re-interpretation of pathology in recent years. I wholeheartedly recommend this collection of monographs and sincerely hope that it will be followed by others like it, since many areas of pathology remain untouched in this beginning effort.

VICTOR A. MCKUSICK

COLLAGEN DISEASES, *Including Systemic Lupus Erythematosus, Polyarteritis, Dermatomyositis, Systemic Scleroderma, Thrombotic Thrombocytopenic Purpura. By John H. Talbott and R. Moleres Ferrandis. Grune & Stratton, New York and London.* $6.50. xvi + 232 pp. + 8 pl.; text ill. 1956.

This monograph, by the Professor of Medicine at the University of Buffalo and one of his fellows, discusses quite comprehensively five disorders of ever-increasing importance to medicine. Since an involvement of connective tissues is the common denominator of these disorders, they are known by the generic designation, "collagen diseases." The term was originally assigned in a *pars pro toto*, and by no means precise, sense by Klemperer of New York City. "Collagen vascular diseases" is an alternative designation. The closely-related and more frequent connective tissue infections—rheumatoid arthritis, acute rheumatic fever, etc.—are not discussed, and rightly so, because of their extensive nature.

Of obscure causation and pathogenesis, these diseases also have in common features which arouse suspicion that disturbance of the immune mechanism is at their roots. Again, they all display protean and wide-spread manifestations which are a challenge to the diagnostician and a fascination to the pathologist. The forms of these diseases tend to be as ubiquitous as connective tissue and blood vessels. Because they involve one tissue in common, there is appreciable overlap of manifestations; and the group is frequently referred to as a "spectrum of diseases." There is reason, however, to believe that each disease is pathogenetically and even etiologically distinct. These acquired disorders of connective tissue discussed by John Talbott and his colleague involve a situation comparable to that of the heritable disorders of connective tissue: despite clinical overlap, there is every reason to conclude that specificity of the several entities exists. The modes of clinical expression of disease in connective tissues are limited.

Talbott and Ferrandis have provided a commendable treatment of the subjects, with illustrations in color, pathological studies, and a total of 540 references to the literature. I know of no monograph to compare with the thorough and authoritative discussion of the five disorders to which this book addresses itself.

V. A. MCKUSICK

VIRAL AND RICKETTSIAL DISEASES OF THE SKIN, EYE AND MUCOUS MEMBRANES OF MAN. *By Harvey Blank and Geoffrey Rake; foreword by Donald M. Pillsbury. Little, Brown & Company, Boston and Toronto.* $8.50. xiv + 285 pp. + 6 pl. + 1 chart; text ill. 1955.

Since the foreword to this book, written by Donald M. Pillsbury, constitutes an excellent review, it is difficult not to plagiarize. Only two hundred and sixty three pages are contained between its covers; yet it brings together in one place just about all that is known, or speculated, about those organisms or particles which we have been in the habit of calling viruses. It is a mine of information about a collection of diseases which, in many instances, are hardly more than mentioned in standard textbooks. For example, the common fever blister is for the first time fully presented; warts are illuminated as never before; the relationship between chickenpox and herpes zoster, between Kaposi's varicilliform eruption and vaccinia and herpes simplex, is clarified; and fascinating but little known entities, such as Brill's disease, orf, and herpangina, are explained.

It should be of especial interest to general practitioners, dermatologists, ophthalmologists, health officers, and medical and sanitary officers of the Armed Forces. Clinical descriptions of diseases are succinct; etiological agents are understandably classified and described; laboratory methods of diagnosis are fully included; and the illustrations, whether in the form of charts, diagrams, electron microscopy, photographs or kodachromes, tremendously enhance the instructional value of the text. Furthermore, the practitioner of medicine will find here all that was known about therapy at the time the book was written. The authors have every right to feel immensely proud of their work.

H. HANFORD HOPKINS

THE CARE OF YOUR SKIN. *By Herbert Lawrence. Little, Brown & Company, Boston and Toronto.* $2.50. xiv + 95 pp. + 4 pl. 1955.

This little book, containing ninety-five pages, was written for the layman to clarify the acne problem, a problem that has confused the public and the medical profession as well. Yet it is questionable that the layman can read this book or that it can alleviate his confusion.

The subject matter is contained in eight chapters,

labelled: Structure of the Skin, Misconceptions about the Causes of Acne, Causes of Acne, Misconceptions about Acne Treatment and Skin Care, What you can do to Help Your Acne, How Acne is Treated by the Skin Specialist, Emotional Problems and their Relation to Acne, and Self-Consciousness about Your Acne.

The pathological anatomy of the disease is well described in the beginning, but from there to the end, the book is a recapitulation of all the many conflicting ideas and opinions which have been expounded without scientific backing for years. It fails to mention the work of Hamilton, who reminded us that eunuchs never develop acne, pointed out the hereditary background in the victims of acne, and showed that males with acne lose it completely when castrated but regain it upon the administration of testosterone. Although the book discusses the role of the endocrine glands in the production of acne, it fails to make clear that all scientific evidence known at present indicates that androgens are the important activating hormones.

The author sets out to deemphasize the influence of dietary factors upon acne, yet spends pages discussing the possible deleterious effects of carbohydrates and fats upon acne sufferers, though hardly a shred of controlled experimental evidence exists to show that the diet has anything to do with this condition.

Much of the book might be called a lecture on hygiene, though its relationship to acne is extremely tenuous. The space given to the attention the acne patient supposedly ought to devote to properly washing his face, to eating the right foods, to avoiding fatigue, to obtaining sufficient sleep, to avoiding worry and emotional tensions, and to ignoring the advice of cosmeticians, is hardly justified by what anyone really knows about the importance or lack of importance of such advice in treating acne.

The physical methods of treating acne with desquamative topical remedies and with x-rays are well covered. Much of what the author says in this regard should have been left out, however, since it deals with niceties of judgment on the part of the individual physician in treating each individual patient.

H. HANFORD HOPKINS

SYMPOSIUM ON THE ANTIMETABOLITES—THEIR MODES OF ACTION AND THERAPEUTIC IMPLICATIONS, 1955. *Proceedings of the Scientific Sessions of the Tenth Annual Meeting, The National Vitamin Foundation, New York City, March 1, 1955.*

11 Contributors. National Vitamin Foundation, New York. $2.00 (paper). 66 pp.; ill. 1955.

Antimetabolite theory provides a basis for the modern approach to the chemotherapy of infection and neoplasia and for the correction of metabolic aberrations. It is important as a tool in the elucidation of metabolic pathways. The scope of the antimetabolite approach is well illustrated in the introduction and the eight articles of this book. Current researches pertaining to antagonists of thiamin, riboflavin, vitamin B_6, pantothenic acid, folic acid, and antagonists of purines and pyrimidines are presented in detail. The historical steps leading to the isolation and identification of a naturally occurring methionine antagonist are outlined. Data are presented on vitamin E antagonists.

The articles review fundamental research at the pharmacological and biochemical level, and illustrate the difficulties encountered and the progress made in attempts to elucidate the biochemical basis for the observable biological effects of metabolic deficiencies. The studies presented serve as prototypes for the current approach in this area of research. This book is an informative supplement to other publications in this field.

A. GOLDIN

THE NATURE OF BRUCELLOSIS.

By Wesley W. Spink. University of Minnesota Press, Minneapolis. $8.00. xiv + 464 pp. + 10 pl.; text ill. 1956.

This book not only reviews the subject of brucellosis; it also gives much new material from the author's laboratory. It appears to be an outstanding study of the subject that should be of great value to physicians, since much of the subject matter is clinical, with protocols on 244 cases. The book should also be of value to veterinarians, to microbiologists, and to workers in the fields of sanitation and public health. It is pointed out that brucellosis is primarily a disease of domestic animals and that, if animal sources could be controlled or eliminated, the human disease would disappear. Despite many obstacles to such a favorable outcome, the situation is rendered hopeful by improvements in the diagnosis and treatment of human cases. There is an excellent bibliography containing 906 references.

WALTER C. TOBIE

PSYCHOSOMATICS.

By Max Hamilton; with a foreword by D. R. MacCalman. John Wiley & Sons, New York. $4.25. xii + 225 pp.; ill. 1955.

This is an unusual and valuable little book that ought to be carefully read by all who work in the field of psychosomatic medicine. Max Hamilton, Senior Lecturer in Psychiatry at the University of Leeds School of Medicine, has put together an urgently needed review of the most important contributions up to 1954. But he has done much more; for in subjecting the entire

field of psychosomatics, with the claims and counterclaims and the elaborate hypotheses of various writers and schools of thought, to a fair, objective, and learned analysis, he has brought a long-needed sense of clarity and balance to this rather confused branch of psychiatry.

After a brief but quite thorough discussion of its theoretical foundations, Hamilton presents an excellent review of the most significant research findings in all the disorders subsumed under the heading of psychosomatics. Asthma, for example, is discussed under the categories of mechanism, psychodynamics, personality of adult asthmatics, emotional factors, asthmatic children, and psychometric research. The principal psychological writings, as well as outstanding physiologic work, are presented. The author examines, in his characteristically balanced and meticulous manner and according to an outline, other respiratory disorders, such as vasomotor rhinitis, the common cold, and even tuberculosis; the psychosomatic diseases of the gastrointestinal system, especially peptic ulcer and ulcerative colitis; cardiovascular conditions including the effort syndrome, functional cardiac arrhythmias, hypertension, and migraine; and disorders of the skin, such as urticaria, rosacea, and atopic eczema (neuro-dermatitis). Chapters on endocrine and metabolic disturbances, rheumatism and cortisone, including a brief discussion of Selye's General Adaptation Syndrome (G.A.S.), precede a final chapter in which Hamilton summarizes his views on the general problems of psychosomatic medicine.

Since the author's style is clear, concise, and free of esoteric jargon, relatively unlabored and interested reading is possible. He is able to present quite fairly the views of such disparate schools as the orthodox psychoanalytic and the rather eclectic psychobiologic orientations. Critical of the unwarranted and flighty excursions into metaphysical speculation of some psychoanalytic writers, he is ready, nevertheless, to acknowledge their contributions. Of special note is Hamilton's equally thorough acquaintance with physiologic medicine and research methodology. By virtue of this latter training, he is frequently able to point out that the conclusions drawn from this or that research project are unjustified. The advantages of a comprehensive approach that combines the disciplines of psychiatry and psychology are well demonstrated in this book. After emphasizing the limitations of the various conflicting personality studies, the inadequacy of much psychosomatic theory, and the failure to prove specificity, Hamilton calls attention to the poorly publicized but promising work on precipitating factors.

The author concludes with the following paragraph: "The neat picture that is given by text-books on scientific method, of examination of data, of induction, deduction and verification of theory, is the finished map of an explored region. It does not describe the process of exploration, which is full of uncertainties, loose ends, unexplored trails, wild guesses and 'lucky chances'; where one leg of a theory rests on solid work while the other flounders in the most uncertain of data. It does not show the giddy changes of viewpoint that may be suddenly brought about by the introduction of a new technique or theory from a distant branch of science. Here, in psychosomatics, we are truly at the frontiers of science. The prospects are exciting."

M. STEINBACH

MIND AND BODY: PSYCHOSOMATIC MEDICINE. *New Enlarged Edition.*

By Flanders Dunbar. Random House, New York. $3.50. xiv + 298 pp. 1955.

Flanders Dunbar was one of the pioneer workers in the "psychosomatic" field; and the first edition of his book, designed to enlighten the lay public about currently held concepts, was published in 1947. The second edition, unfortunately, is occupied with extending these concepts into additional medical areas (including cancer, dental troubles, etc.) rather than with revising the data that could not be validated. Thus, while there is much commendable material in this book, there is much that is, in our present state of knowledge, scientifically objectionable. For the lay audience that is addressed, it is amazingly lucid and intelligible, with abundant clinical anecdotes to illustrate various types of internal psychological and external situational problems to which people react with physical symptoms. And it convincingly illustrates, with many examples, how patients may, through conferences with a psychiatrist, understand their pathological modes of reaction and evolve more rational ways of dealing with their problems than symptom formation offers. These points are made over and over, in a way that must have incalculable educational value for the general public. But gone are the days when physicians could explain complicated medical illnesses solely as psychological reactions, interpreting symptoms symbolically. The recent trend in psychosomatic research has been towards multi-dimensional studies with a great deal more effort to elucidate the pathophysiological mechanisms involved and to study the inter-relationships of these mechanisms with psychological factors and changes in affect or mood. The author acknowledges some of the complexities of research and treatment in the last few paragraphs of the book, but cannot undo such earlier remarks as: "Faced with the inevitability of conflict in his own mind, first with his parents and then with his partner in his marriage, he is likely to get diabetes" (p. 48); "Unable to decide what to do next, he had his second attack of rheumatic fever" (p. 79); and "Hemorrhoids are an even more avoidable expression of this sort of basic conflict than colitis, and represent an even more infantile personality." While I

do not know whether or not such statements are relatively harmless for lay readers, I can say that they might evoke physiologically bona fide, non-hysterical seizures in our medical colleagues, or at least that, in promoting distrust of the psychiatrist's scientific objectivity, they could set back the trend toward collaborative (internist and psychiatrist) clinical management of a variety of medical problems. Perhaps Dunbar should not have tampered with the first edition of the book, but should, rather, have left it as an historical testimonial to the enthusiasm and theories of the early post-war years.

FREDERICK J. ZIEGLER

DOCTORS' OFFICES AND CLINICS, *Medical and Dental. By Paul Hayden Kirk and Eugene D. Sternberg. Reinhold Publishing Corporation, New York.* $12.00. 218 pp.; ill. 1955.

This is one of a series of books by the same publisher covering special architectural problems. Others in the series deal with hospitals, motels, TV stations, shopping centers, etc. The distinctly modernistic styles recommended for doctors' and dentists' offices are consistent with the rapid advances of medicine; but one might wish for a flavor of tradition, since medicine has that, too.

VICTOR A. MCKUSICK

PSYCHOLOGY AND ANIMAL BEHAVIOR

MAN MEETS DOG.

By Konrad Z. Lorenz; translated by Marjorie Kerr Wilson; illustrated by Annie Eisenmenger and the author. Houghton Mifflin Company, Boston. $3.00. xii + 211 pp.; ill. 1955.

This is a delightfully written book about dogs in general and about Lorenz's own dogs in particular. The author's method of description is completely anecdotal. In the twenty-one chapters a large variety of subjects is covered, among them: the origins of fidelity, training, breeding, canine customs, comprehension of language, the animal with a conscience, and fidelity and death. There are also two chapters on the cat.

The author brings to the book the qualifications not only of an experimental zoologist, but those as well of a man who has had much experience with dogs and who loves them deeply. Lorenz's love for dogs lends warmth and charm to the book, but it produces some rather naive anthropomorphisms as well. This volume is clearly intended for the animal lover, and as such it is informative and enjoyable. Pen and ink illustrations done by Annie Eisenmenger and the author on the margins of almost every page add charm to the book.

SONIA F. OSLER

INFORMATION THEORY IN PSYCHOLOGY. *Problems and Methods. Proceedings of a Conference on the Estimation of Information Flow, Monticello, Illinois, June 5–9, 1954, and Related Papers.*

Edited by Henry Quastler. The Free Press, Glencoe. $6.00. xii + 436 pp.; ill. 1955.

This volume contains 30 papers, most of which were presented at a five-day conference in 1954 on the Estimation of Information Flow. The conference and the publication of its proceedings are testimonials to the recent importance and influence of information theory in the study of psychological problems. My impression of this volume, however, is that it belies its title. Rather than systematically displaying the application of information theory and information measures to psychological problems, reviewing the fruits of such application to date, or comparing the value of this approach with the value of other approaches, much of this work is devoted to problems facing the user of information theory himself. This is especially true of the section on information measures, to which about a third of the book is devoted; but many of the items in the section entitled Information Theory in Psychology, the largest section of the four, make only tangential contact with concepts, problems, and methods as the psychologist ordinarily uses them. I am afraid that this compendium will disappoint anyone who reads it with the hope of learning what information theory can contribute to the psychological study of behavior.

CHARLES N. COFER

PRESENT-DAY PSYCHOLOGY. *An Original Survey of Departments, Branches, Methods, and Phases, Including Clinical and Dynamic Psychology.*

Edited by A. A. Roback, with the collaboration of 40 experts in the various fields. Philosophical Library, New York. $12.00. xiv + 995 pp. + 4 pl.; text ill. 1955.

There are many symposia and collections of readings available in the various fields of psychology, but it is safe to say that none of them matches this one in variety of content. But variety is not without disadvantage; and, in this case, it is difficult to determine just what the editor intended his book to be or how he instructed his contributors.

The 40 selections are classified into five groups. The first, Topical Departments of Psychology, contains nine chapters treating neurology, sensation, perception, cognition, attention, memory, emotion, personality, and character. The Branches of Psychology, as treated in the eleven chapters of Part Two, are Child, Adolescent, Educational, Comparative, Abnormal, Social, Applied, Military, and Historical Psychology, as well as Psychometrics and Parapsychology. Yet Dynamic and

Clinical Psychology, which presumably are "branches," get a full section of the book to themselves—12 chapters concerned with psychodiagnosis, projective methods, psychoanalysis, psychosomatics, clinical psychology, psychotherapy, psychodrama, speech, hypnotherapy, problem children, Adlerian theory, and "interpersonalism." The Methods section is slim (two chapters); and the final section on Psychological Borderlands and Humanistics yields chapters on literature, linguistics, aesthetics, art, values, and religion.

Obviously, no one reviewer is competent to evaluate adequately this wide array. I have sampled it, however, and have read critically a number of selections concerning fields in which I have some competence. For the most part they were disappointing. They are neither reviews of the literature, as one would get in a handbook, nor adequate elementary surveys that one might use for undergraduate students. Yet they presume knowledge of and concern with problems, issues, and names likely to be familiar to the layman. While there are some good selections in the volume and while it includes discussions of topics not often treated elsewhere, the balance, in my judgment, swings to the unfavorable side.

CHARLES N. COFER

CURRENT TRENDS IN PSYCHOLOGY AND THE BEHAVIORAL SCIENCES. *Eighth Annual Conference on Current Trends in Psychology Held at the University of Pittsburgh, 1954.*

University of Pittsburgh Press, Pittsburgh. $4.00. 142 pp.; ill. 1955.

Following an introduction by Robert Patton, this book presents the following six papers: Psychology and Behavioral Science (John T. Wilson); Some Potential Contributions of Anthropology to Psychology (Clellan S. Ford); The Science of Learning and the Art of Teaching (B. F. Skinner); Reduction (Gustav Bergman); The Individual from Conception to Conceptualization (Frank A. Beach); Toward a Science of Neurology—Method and Data (Karl Pribram).

In the Introduction, Patton points out that the general topic for this conference "concerns the relationship between psychology and some of the other behavioral sciences." Because areas of science continually overlap, clarity of concepts becomes essential for proper communication and for the enrichment of one discipline by another. By way of illustration, Patton shows how the concept of stress has been used to mean different things by psychologists and physiologists. He then proceeds to develop a definition of stress that would be satisfactory to all and that would, in fact, provide an anchor for more productive research.

Each of the papers that follow treats a different aspect of the interdisciplinary approach to the study of behavior in an interesting and informative fashion. The most provocative of all is the paper by Skinner, in which is proposed a method of elementary school teaching embodying the findings from the extensive researches on instrumental conditioning. Whether Skinner's recommendations can be accepted in toto or not, the the face validity of some of his points and the new vistas opened by his proposal call for serious consideration of his ideas.

Two other papers, one by Beach and the other by Pribram, are especially thought-provoking. But I do not intend to detract from the value of the others, which, combined with these three, make up a worthwhile work on the relation of contemporary psychology to other behavioral sciences.

SONIA F. OSLER

STUDENT'S WORKBOOK, *for Use with* Psychology, *by Wickens and Meyer.*

Prepared by Irwin A. Berg. The Dryden Press, New York. $1.35 (paper). x + 182 pp. 1955.

TEACHER'S MANUAL *to Accompany the Wickens' and Meyer's* Psychology.

By Harry P. Bahrick. The Dryden Press, New York. Free to teachers. ii + 70 pp. 1955.

Each Workbook chapter, paralleling the corresponding chapters of the textbook, has four sections. In Orientation the problems of behavior discussed in the respective chapters of the text are highlighted by pertinent new material examined from a point of view different from that presented in the text. The other sections contain Terms and Concepts; Objective Self-Test Exercises; and Demonstrations, Exercises and Projects.

Bahrick's *Manual* for the teacher using the Wickens and Meyer text contains multiple-choice and true-false questions; discussion questions; and, for some chapters, suggestions for classroom demonstrations and experiments, besides a bibliography of recent literature relevant to the teaching of general psychology and a list of recommended films.

ANNELIES A. ROSE

A STUDY OF THINKING. *A Publication of the Harvard Cognition Project. A Wiley Publication in Psychology. By Jerome S. Bruner, Jacqueline J. Goodnow, and the late George A. Austin; with an appendix on Language by Roger W. Brown. John Wiley & Sons, New York; Chapman & Hall, London.* $5.50. xii + 330 pp.; ill. 1956.

A general and probably essential technique used to bring order and continuity into experience is "cate-

gorizing." While we are capable, for example, of distinguishing species of dogs and even individual members of any one species, it is often enough, in our thinking, perceiving, and remembering, to refer only to the general category—i.e., to "dogs." That we do this so easily is apt to mask the rather amazing amount of variation that is ignored in favor of the common characteristics basic to the concept, "dog."

These authors, duly impressed with the role played by categorizing in human behavior, devote three chapters to documenting and explaining this role. Major emphasis of the book, however, is on the results of some 20 previously unpublished studies concerned with the strategies people use in discovering the properties of instances that are relevant to concepts. Subjects of these studies examined a series of instances in order to discover the essential characteristics of the concept involved. This is here termed "concept attainment" and is distinguished from "concept formation." The tasks, designed for the purposes of the experimenters, permitted variation in a number of dimensions. This report is particularly concerned with the strategies used in solving problems and the characteristics of problems which led to the choice of different strategies. The roles of information theory and decision theory are significant in the authors' thinking; some of the variations in experimental procedure and some of the ways of describing and evaluating strategies show these influences.

To describe the methods, problems, and results further would require too long a discussion. Suffice it to say that the volume provides interesting and stimulating material for one interested in cognitive processes. One should, perhaps, be cautioned that it is by no means certain how far the results concerning strategies of concept attainment may be generalized beyond the experimental problems and subjects used in this project. This caution seems appropriate in view of the authors' extensive use of the hypothetical anecdote to illustrate points. The anecdote implies a generalization, though perhaps unintentionally. One of the most rewarding features of the book is the appendix written by Roger W. Brown. It is a lucid description of language and linguistics in which emphasis falls on the role of language as a categorization process.

CHARLES N. COFER

THE PSYCHOLOGY OF THOUGHT AND JUDGMENT. *By Donald M. Johnson. Harper & Brothers, New York.* $6.00. xi + 515 pp. 1955.

The purpose of this book, as given by the author, is to provide "an integration of the psychology of thought, aiming at breadth rather than the exploitation of any special theoretical approach." By and large the author sticks to his plan, especially with respect to extensive coverage.

The book consists of thirteen chapters; and all but the first and last concern themselves with a review of studies, both observational and experimental, of thinking, of problem solving, and of judgment. The material can be roughly divided into three sections: (1) the influence of perception, motivation, and learning upon thinking; (2) the analysis of the thought process; and (3) the variables operating in the process of judgment. Within each of these sections the reader will find a comprehensive report of pertinent psychological research, with emphasis on the work of American investigators. Each chapter is followed by a bibliography.

That the author avoids becoming embroiled in theoretical formulations has necessitated a less than cursory treatment of the rich history of his subject, and the book accordingly, lacks perspective. Everything stands out with equal boldness, and the reader has to fend for himself to integrate the ideas into some sort of a whole. Because of his avoidance of theoretical formulation, the author does not succeed in one of his stated objectives—the integration of the field of thought. The generality required for integration would, of necessity, constitute a theoretical commitment. Yet this lack is not altogether without advantage; for it permits the reader to examine data that have not been selected for, or compressed into, a specified framework. Moreover, since three or four other books on "thinking" published during the last decade lean heavily toward the theoretical approach, the empirical method chosen by this author may well serve to complement the already existing body of literature in this area.

The refreshingly simple and direct style of the book should be a great aid to the newcomer to the field. This reviewer feels that simplicity is sometimes carried to extremes, especially in certain definitions; but, on the whole, over-simplification is to be preferred to the needless complexity of many formulations found in psychological writing.

Two major areas—the developmental aspects of thought and pathological thinking—are not treated by Johnson. As the book contains over 500 pages, however, it seems evident that no ordinary volume can, at the present state of knowledge, cover the entire field of thinking. Every author has the prerogative to make his choices. The book has much to offer to anyone desirous of acquainting himself with the methods and findings of research conducted in the area of thinking and judgment.

SONIA F. OSLER

METHODS IN PERSONALITY ASSESSMENT. *Human Behavior in Complex Social Situations.*

By George S. Stern, Morris I. Stein, and Benjamin S.

Bloom. The Free Press, Glencoe. $6.00. 271 pp.; ill. 1956.

This book considers the problem of prediction of performance. Its major contribution is an emphasis upon, and an elaboration of, the criterion problem, which involves knowledge of the relevant variables that affect adequate performance. The authors refer to two major efforts to predict: the project conducted by the Office of Strategic Services during World War II in an effort to predict the performance of intelligence personnel, and the Veterans Administration project conducted shortly after that war in an effort to predict performance of clinical psychologists. Despite the fact that very experienced and highly respected psychologists were involved in each of these projects, their efforts at prediction failed. And the authors of this book hold that the cause of failure lay in uncertain and inadequate criteria.

To tackle the criterion problem effectively, the Analytic Method of Assessment is proposed. This method involves several steps, beginning with intensive interviews and lengthy conferences with those who will ultimately do the assessing and followed by equally intensive studies of the individuals to be assessed. The latter studies involve depth interviewing, writing and evaluating of biographical material, and a variety of projective techniques. The description of the method is followed by two illustrative studies utilizing analytic procedures.

At this point the authors declare their awareness of the two disadvantages of their proposed procedure—namely, the excessive length of time it requires and the complexity of the procedures involved. For these reasons they propose three alternative methods of assessment: (1) the empirical, (2) the synthetic, and (3) the configurational approaches. Despite the new terminology, the procedures involved in these methods are not basically different from those used by assessment psychologists for many years. Furthermore, they all revert to a reliance upon questionnaire or inventory type tests, the weaknesses of which have been demonstrated in the past and are well known to the authors.

One is forced to wonder to whom this book is addressed. Many chapters assume a good deal of psychological sophistication; but, on the other hand, there are sections in which the authors discuss the most elementary aspects of interviewing ("... it is incumbent upon the examiner to establish a setting in which the subject can talk freely and behave comfortably") or refer to the Rorschach as an inkblot test, consisting of ten cards, five achromatic, etc., etc.

As stated earlier in the review, the important contribution of the book is its forceful statement of the criterion problem in psychological assessment, a problem that still remains essentially unsolved.

SONIA F. OSLER

BEHAVIOR AND DEVELOPMENT IN CHILDHOOD.

By Alfred L. Baldwin. The Dryden Press, New York. $6.25. xviii + 619 pp.; ill. 1955.

This book is, in many ways, a unique addition to the numerous existing textbooks of child psychology—some written for the reader with an adequate scientific background, some for the parent or teacher.

The division indicated in the title is carried out in the presentation of the problems. The first and larger part of the book, Behavior in Childhood, tries to show how the child, at different levels of maturity, behaves in specific situations and how he differs from the mature adult, whose behavior is characterized by objectivity, differentiation, and emotional stability. The needs and abilities of the child, cognitive processes and goal-directed behavior, and the mechanisms of social control and self-control are discussed in this section. The second part, Development in Childhood, describes and tries to explain the changes that take place in the personality of the child as the result of maturation and of learning in culture and society.

Although the author feels that, at present, no theory adequately explains child development, he discusses psychological problems in the framework of general behavior theory, as well as in the light of a critical selection of Freudian and neo-Freudian psychoanalytic concepts. Baldwin's own analysis and interpretation of childhood behavior is made largely in terms of the characteristics of concreteness and rigidity or, to use his concepts, of undoing and detachment. Applying these concepts to such behavior as making amends for an act, forgiving, or recapturing one's pride after a shameful incident, the child, bound to the concrete situation and unable to detach himself from the problem as he has defined it, has to turn back to the beginning of his action and to undo his behavior; while the mature adult, more abstract and flexible in his approach to problem-solving, needs only to reestablish the essential relevant characteristics of his behavior. Both these concepts are applicable to a variety of child behavior and are testable.

Throughout the book the discussion is based on very well selected and well presented experimental evidence which is related to the casual observations and intuitive understanding of children's behavior by parents and teachers.

Concepts and principles of general psychology are well integrated with the discussion of the problems of this field of specialization and application. For the non-psychologist the book may serve as an introduction to general psychology based on the scientific study of human development.

ANNELIES A. ROSE

THE ADULT-CHILD INTERACTION TEST: *A Projective Test for Use in Research. Monogr. Soc. Res. Child Developm., Vol. XVII, Ser. No. 55, No. 2, 1952.*

By Theron Alexander. Child Development Publications, University of Illinois, Champaign. $4.50 (paper). v + 40 pp. + 8 cards. 1955.

This is a projective test, similar to the Thematic Apperception Test in that it consists of pictures (eight in this case) about which the subject is asked to tell a story containing the following information: (a) what is going on in the picture; (b) what brought the situation about; and (c) what the outcome will be. The test is suitable for children and adults. It is designed primarily to yield information regarding children's perception of adults and the perception of children by adults. It may be administered individually or in groups.

The author suggests a method of analysis following two major dimensions: (a) apperception and reasoning, and (b) motivation and emotion. Each of these is further sub-divided into smaller categories. Two illustrative protocols, one of a boy eleven years old and the other of a woman thirty-one years old, are analyzed in accordance with the suggested schema.

The author describes the test as suitable for research, rather than for clinical use. This is especially appropriate; for since it has so far had very limited application, little is known about its usefulness in a clinical setting. On the basis of its essential similarity to the TAT, however, one would expect it to be a useful projective tool for eliciting information in the area of adult-child interactions.

SONIA F. OSLER

PSYCHOLOGY IN INDUSTRY. *A Psychological Approach to Industrial Problems. Second Edition.*

By Norman R. F. Maier. Houghton Mifflin Company, Boston, New York, Chicago, Dallas, Atlanta, and San Francisco. $5.50. xvix + 678 pp. + 2 pl.; text ill. 1955.

Traditionally, industrial psychology may be said to start with the publication, in Germany in 1912 (translated in the United States in 1913), of a volume entitled *Psychology and Industrial Efficiency*. The author, Hugo Münsterberg, had been invited to Harvard by William James and, in his later years, was director of the Harvard Psychological Laboratory.

In 1932, Morris S. Viteles published *Industrial Psychology*, which is still a classic in the field. In the twenty years that had elapsed since Münsterberg, industrial psychology had actually moved out of a book and into industry. Its application tended to be restricted to matching men and occupations by the use of various kinds of tests and questionnaires. Job analysis, worker analysis, and problems of fatigue, monotony, and safety were the core of the new applied science.

Today, there are a number of good textbooks in the field, and Maier's is one of the best among them. His book can be read with pleasure and profit by both the student and the industrial person who is interested in the management of men.

The scope of the application of psychology in management and industry can be appreciated, even if one only lists some of the subjects covered in this book. On the one hand, there are chapters with industrial appeal: The Use of Selection Tests, Industrial Training, Psychological Factors in Labor Turnover, Fatigue, Safety, Supervisory Leadership, Measuring Proficiency, Motion and Time Analysis, and Counseling and Interviewing, among others. And, on the other hand, there are chapters of sound psychology: Causation in Behavior, the Psychology of Attitudes, Morale and Motivation, Frustration, Individual Differences, etc. The non-psychologist may be surprised to discover how extensively psychology is used in industry and how much sound research is going on in the field.

An additional feature of Maier's book is its presentation of novel laboratory exercises, including role-playing, "buzz" groups, group problem-solving, practice in discussion leadership, and others.

This book can be recommended for its breadth of coverage and for its readability. For the advanced reader, there are numerous references to more detailed studies.

LUIGI PETRULLO

PHRENOLOGY FAD AND SCIENCE. *A 19th-Century American Crusade.*

By John D. Davies. Yale University Press, New Haven; Geoffrey Cumberlege, Oxford University Press, London. $3.75. xvi + 203 pp.; ill. 1955.

John D. Davies' informative monograph illuminates a hitherto neglected corner of American cultural history: the growth, flowering, and decline of popular interest in phrenology. Today regarded as a refuge for charlatans who, for a fee, read character from bumps on the head, it began as a scientific hypothesis which can be said to have paved the way for a physiological psychology. Moreover, for a period, phrenology drew support from men of estimable reputation in American medicine, science, and national life; boasted a journal with the largest circulation extant; and influenced education, psychiatry, and social reform.

Its originator, the Viennese physician Franz Joseph Gall, made important anatomic contributions; his method of brain dissection was a decided advance beyond the conventional method of horizontal sectioning. His system was based upon (1) a division of the

mind into numerous independent faculties (borrowed from the Scottish school of psychology); (2) a localization of these "faculties" in discrete "organs" (that is, areas) of the brain; (3) the assumption of a correlation between the size of the "organ" and the strength of the "faculty;" and (4) a conviction that "organ" growth determined the configuration of the overlying skull and that, because of this, psychological traits could be determined from palpation of the cranium.

It is easy now to recognize that the errors in his system were both conceptual and methodological. The "faculties" were mere semantic inventions that capriciously divided mental functioning; without psychological reality, they could have no anatomical locus. The method employed was the search for outstanding examples of mental types; cranioscopy of the individual "localized" the characteristic to adventitious cranial protuberances. Thus, only positive instances need be employed; the number and overlap of other "faculties" could explain away apparent discrepancies.

Yet Gall had made an important contribution. He propagandized the ancient dictum that the brain is the organ of the mind until it took on new respectability. If his method seems naive to us, his investigation predated statistical sophistication. His concept of localization of "faculties," albeit non-existent ones, was the forerunner of modern cerebral localization. Flourens' classical experiments on the cerebellum were published in disproof of the phrenologist's ex cathedra pronouncement that "amativeness" was to be found there. Broca's localization of the speech center in the posterior end of the third frontal convolution was in part guided by the phrenological charts that had placed "language" in the subfrontal orbital area. Some fifty years were to intervene between Gall's postulation of localization and the experiments of Hitzig and Ferrier that established the existence of the cortical motor area.

But if Gall had proposed a scientific hypothesis, his disciple, Spurzheim, and the later convert, Combe, brought to America a philosophical elaboration of phrenology into a doctrine of social reform. If the brain was the organ of the mind and psychological attributes a consequence of its uneven development, the criminal and the insane were not to be condemned, but treated instead, for their biological inadequacies. If hypertrophic faculties could be held in check, and underdeveloped ones stimulated by proper training and experience, then one had merely to perform cranioscopy, consult the phrenological charts, and prescribe for the ultimate perfectability of human nature. The implicit denial of original sin and of moral responsibility were readily sensed by the orthodox clergy; throughout its career, phrenology was attacked as a subversive doctrine.

It was this optimistic view of the educability of man that drew to the ranks of phrenology so many supporters in a democratic, vigorous America. But once it ventured into the public forum, phrenology became the property of bleary-eyed sentimentalists, enterprising adventurers, and quacks. It ceased to be of interest to science, but its function had been served. It faded from the public scene as well, once a new and challenging movement of social reform—abolitionism—became the battleground of moral conscience.

The bulk of this fascinating monograph is devoted to an analysis of America's acceptance of phrenology and of the resulting impact on the intellectual life of the country in the 2nd quarter of the 19th century. The author is an historian of culture, not of science. His book can be heartily recommended to scientist and layman alike, but the student of science will wish to refer to Temkin's exemplary essay on "Gall and the Phrenological Movement" (*Bull. Hist. Med.*, 21: 275. 1947) and to Dallenbach's provocative comparison of the history of phrenology with that of psychoanalysis (*Amer. J. Psychol.*, 68: 511. 1955). It was Gall's contemporary, Goethe, who wrote: "The history of science is science itself."

LEON EISENBERG

PSYCHICAL RESEARCH.

By R. C. Johnson. Philosophical Library, New York. $2.75. viii + 176 pp. 1956.

This small volume by R. C. Johnson is written "for the ordinary thoughtful person . . . who would like to understand what psychical research is all about." The author covers the entire field of spiritualism with chapters on Historical Background, Telepathy and Clairvoyance, Precognition and Retrocognition, Object-reading or Psychometry, Psycho-kinesis and Poltergeist Phenomena, Materialisation Phenomena, Apparitions and Hauntings, Mediumship, The Problem of Survival, and The Importance of Psychical Research. He presents the important data in favor of the above "paranormal" phenomena and introduces the reader to a fairly comprehensive review of the whole subject.

This book makes interesting reading, though it is somewhat fantastic to one who has never had an experience which suggested "paranormal" psychic activity, has never come in contact with any "sensitives," and has always regarded such claims as incredible—frequently as bordering on the fraudulent. The author cites examples from many sources, particularly from the voluminous reports of the *Proceedings and Journal of the Society for Psychical Research* compiled during the past 70-odd years. He is quite earnest and certainly sincere in completely accepting the whole range of spiritualistic phenomena. He has written extensively on the subject, knows its literature thoroughly, has conducted considerable research himself, and has con-

tributed such concepts as "psychic ether" to explain many of the events recorded above. He sounds quite scientific when discussing the work of J. B. Rhine, head of the Department of Parapsychology at Duke University. He quotes many well-known and respected people—such as William James, Sir Oliver Lodge, and Sir Richard Crookes—and cites "unimpeachable" evidence from apparently intelligent witnesses.

I am certainly in no position to dispute the authenticity of the recorded facts or to question the reliability of the given testimony or the results of psychical research. Although impressed by the erudition of the writer, I could not help feeling, after several days of thoughtful consideration, that there was something quite impossible and fantastic about the material and the reasoning so completely accepted by the author. Most of the recorded incidents occurred many years ago; and there are very few, if any, survivors. Secondly, the illustrious names connected with psychical research were somehow mostly Englishmen who were attracted to the field very late in their lives. Again, many of the "paranormal" phenomena can be explained quite readily on the basis of coincidence, suggestibility, and psychopathological phenomena—such as delusions, illusions, and hallucinations—rather than by telepathy, clairvoyance, precognition, etc. The activities of mediums have been repeatedly exposed as quite fraudulent, and their genuine "trances" can best be understood in terms of auto-hypnosis and hysterical states. The work on parapsychology at Duke University is rather equivocal and, thus far, only suggests the operation of extra-sensory perception as a subconscious or unconscious psychological function, not as anything supernatural or etheric.

For Johnson the existence of a psi faculty (ESP), as well as all the phenomena postulated by spiritualists, is basic and indisputable. He believes implicitly in the testimony and writings of fellow believers. The so-called experimental work in psychical research, according to him, only substantiates the operation of an extra-corporeal mentality. For him, ideas have a substantive form and are in fact more real than material objects. Since the entire materialistic world is only a creation of the mind, it is not difficult, for him, to conceive of ideas, telepathic communication, spirits, psychic ether, discarnate minds, psi faculty, survival after death, etc., as being similar to the familiar environment our senses perceive. Once we accept the author's premises, then the existence of an extra-physical cosmos with the various extra-sensory phenomena described in this volume seems not too fantastic or implausible. But to do that is to leave this world of reality and the firm basis of scientific thought for a speculative journey in an imaginary vehicle to a never-never-land.

M. STEINBACH

HUMAN BIOLOGY

MAN'S ROLE IN CHANGING THE FACE OF THE EARTH. *International Symposium, Wenner-Gren Foundation for Anthropological Research.*

Edited by William L. Thomas, Jr.; with the collaboration of Carl O. Sauer, Marston Bates, and Lewis Mumford. The University of Chicago Press, Chicago. $12.50. xxxviii + 1193 pp.; ill. 1956.

Although this earth has undergone great and innumerable changes during its several billion years of existence, none have been so dramatic or so quickly effected as those caused or wrought by man since his gain of partial control over his environment. The age of atomic energy promises greater changes, and it is clear that an appraisal of the situation is desperately needed if man is to live in fruitful happiness.

The Wenner-Gren Foundation for Anthropological Research has undertaken such an appraisal in a symposium that attempts to assess "man's capacity to transform his physical-biological environment" and to examine "his cumulative and irreversible alterations of the earth." The symposium opens with the question: "What has been, and is, happening to the earth's surface as a result of man's having been on it for a long time, increasing in numbers and skills unevenly, at different places and times?" As Paul Fejos points out in the foreword to this book, three interrelated factors are involved: the earth's resources, the effect of population on these resources, and man's differing cultures. A meaningful appraisal of these factors requires the thought and constructive evaluation of many men of varied disciplines and modes of investigation; and it is fair to say that the success of the symposium called for this purpose is evident throughout the nearly 1200 pages of this volume. Anthropology is represented as a broadly conceived and immensely fascinating science, a discipline which ever keeps man in the forefront of its thought at the same time that it is aware of the influence of environment on man, and which attempts to assess the interrelation and interdependence of two parallel evolutions—that of man and that of his environment.

The 50-odd papers, with accompanying discussions and summaries, are grouped into three sections: Retrospect, Process, and Prospect. The first section deals with man's tenure on earth from earliest recorded times to the present. It includes discussions of cultural differences and expansions; of changing economies from subsistence levels to commercial developments; and of patterns of life in Europe, Asia, and Africa from their most primitive expression to that of highly organized urban dominance. Under Process are included considerations of physical phenomena which alter the environment and indirectly affect man, though major emphasis is given to man's effect on the waters, soils, and organisms of the earth. It is this section, with seven of the papers grouped into a sub-section called Modification

of Biotic Communities, which will probably prove of greatest interest to biologists in general. The papers and discussions under Prospect center around the limits of man and of the earth. Population dynamics and limitations of matter and energy are major topics here. This section is followed by the comprehensive summaries of Carl Sauer (Retrospect), Marston Bates (Process), and Lewis Mumford (Prospect).

Any attempt to appraise this volume is certain to fall short: the book covers an immense area of research and learning, it is uneven in quality, and gaps in our knowledge and understanding are evident. But it is an opportune, a needed, and a fascinating book. Our spiralling population; our ready and rapid means of transportation; our diminishing natural resources; and our differing and often conflicting cultural, economic, and political mores and patterns require understanding, planning, and cooperative action if we are to be prepared for future dilemmas. But the words of Mumford suggest that there is hope: "The awful omniscience and omnipotence of our science and techniques would turn out to be more self-destructive than ignorance and impotence if the compensating processes of life did not foster a new kind of personality, whose all-lovingness will in time offset these dangerous tendencies. We are now at a point where over two billion people have become our neighbors, and we shall have to learn all over again, without going back to our Stone Age ancestors, what the love of neighbors means. . . . If we approach the earth and man in a spirit of love, we shall respect their individuality and treasure the gifts to personality that organic variety itself brings with it. . . . Not power but power directed by love into forms of beauty and truth is what we need for our future development. Only when love takes the lead will the earth, and life on earth, be safe again." Such a point of view can hardly be fostered by an amoral science.

C. P. SWANSON

ON HUMAN COMMUNICATION. *A Review, a Survey, and a Criticism.*

By Colin Cherry. Technology Press, M.I.T.; John Wiley and Sons, New York. $6.75. xiv + 333 pp.; ill. 1957.

The highly intelligent and learned author of this fascinating volume is an engineer on the staff of the Imperial College, University of London. He is unusually competent to discuss such difficult material, having extended his own investigations into all of the fields involved, including mathematics, electrical telecommunication, lingustics, and experimental psychology.

The book itself is "A Review, A Survey, and a Criticism" which appears as the first volume in a series entitled Studies in Communication. As stated by the author in his brief Preface, ". . . if it gives some notion of the relations between the diverse studies of communication, of the causes and the growth of this modern interest, together with some idea of the unification which exists (and even more important, the differences of opinion, controversies and lack of unification) then this book will have achieved its object."

The field covered is so complex and involves so many disciplines that one somehow feels the only proper review would be one compiled by a group of experts representing all the areas involved. It is, then, with great admiration that one reads this discussion of mathematics, neurophysiology, psychology, sociology, information theory, linguistics, physics, etc., which results from a remarkable process of filtration and integration in a highly educated and creative mind. It ought now to be fairly obvious that the questions dealt with here are relevant to various problems of wide interest. They include the differences between human and animal communication, the meaning of "meaning," the difference between brain and machine, the logic of human language, the role of information theory in experimental psychology, among others.

The relevance of information theory to certain biological problems is of special interest among these questions. Recent considerations and researches have suggested that the concept of entropy, or amount of information, plays a basic role in information, communication, and cybernetics. These new theories, based on the unique contributions of Fisher, von Neumann, Wiener, and others, have been shown to be applicable to the analysis of such various functions of living organisms as metabolism, differentiation, and growth, for example. As Quastler has pointed out, the "information" of the theory can be used "in connection with all operations which aim at decreasing such quantities as disorder, entropy, generality, ignorance, indistinctness, noise, randomness, uncertainty, variability, and at increasing the amount or degree of certainty, design, differentiation, distinctiveness, individualization, information, lawfulness, orderliness, particularity, regularity, specificity, uniqueness."

It remains to point out that C. Cherry has certain literary, as well as scientific, talents. A quotation, taken from the section of the book on "meaning," will serve to illustrate these. The author states, "'Meaning' is a harlot among words: it is a temptress who can seduce the writer or speaker from the path of intellectual chastity. There are many like her. Our language is fraught with such words of easy virtue; words like 'true,' 'value,' 'instinct,' 'entity.' These are everyday words, and their ambiguity is such that high-sounding statements may easily be made, having little content." Such meaningless statements are certainly not found in this book.

R. G. GRENELL

A SOLOMON ISLAND SOCIETY. *Kinship and Leadership among the Siuai of Bougainville.*

By Douglas L. Oliver. Harvard University Press, Cambridge. $10.00. xxii + 533 + ii pp. + 16 pl.; text ill. 1955.

This is not "just another ethnography." It is an intimate account of a people in the rain forests of southwest Bougainville, a population of about 4700. The author selected for study a segment of this population with whom he spent the greater part of a year. There is, probably, no more intensive, subtly analytical, judicially selective, and well-balanced account of any tribe.

Concluding sections give the author's inferences and surmises regarding unrecorded historic backgrounds and a synthesis of his findings, including a characterization of tribal personality traits. He carefully distinguishes observed phenomena and behavior from inferences based on these.

A glossary of native terms used in the text, or inclusion of them in the index, would save the reader the trouble of hunting for the page on which a term was first used and defined.

WILSON D. WALLIS

MAKING THE MOST OF MARRIAGE.

By Paul H. Landis. Appleton-Century-Crofts, New York. $5.50. xii + 542 pp.; ill. 1955.

FAMILY, *Socialization and Interaction Process.*

By Talcott Parsons and Robert F. Bales, in collaboration with James Olds, Morris Zelditch, Jr., and Philip E. Slater. The Free Press, Glencoe. $6.00. xviii + 422 pp.; ill. 1955.

These two books on the sociology of the modern American family agree that the American family is changing in function, but not disappearing or losing importance in society.

Parsons and Bales use the American family as a point of departure from which they move into general discussions of such topics as the socialization of children and role differentiation in small groups. Their emphasis throughout is on theory, often highly original, sometimes disturbingly removed from data; however, they cite some pertinent sociological statistics, cross-cultural studies, and laboratory experiments.

Landis' book is written as a text for marriage and family courses. It discusses such varied topics as dating, finance management, child-training patterns, divorce, and others. These discussions are tied closely to empirical studies and make use of largely traditional, theoretical explanations.

CLINTON DE SOTO

BIOMETRY

SYMPOSIUM ON MONTE CARLO METHODS. *Held at the University of Florida, conducted by the Statistical Laboratory, sponsored by Wright Air Development Center of the Air Research and Development Command, March 16 and 17, 1954.*

Edited by Herbert A. Meyer. John Wiley & Sons, New York; Chapman & Hall, London. $7.50. xviii + 382 pp.; ill. 1956.

The Monte Carlo Method involves a combination of sampling theory and numerical analysis. It is being used extensively, usually with the aid of electronic computers, in the solution of certain deterministic and probabilistic problems that are difficult, if not impossible, to solve analytically. The method is being applied successfully to problems in statistics, physics, mathematics, and, more recently, Operations Research.

The first symposium on the Monte Carlo Method was held in Los Angeles in 1949; and its proceedings were published under the name, *Monte Carlo Method* (National Bureau of Standards, Applied Mathematics Series 12, 1951). The second symposium, held at the University of Florida in 1954, produced the present book.

Part I (282 pages) contains the papers presented at the symposium, most of which have been rewritten. The paper by A. W. Marshall serves as an introduction. He briefly discusses the definition of Monte Carlo Methods, then reviews the progress of Monte Carlo Methods from 1949 to 1954, and finally gives detailed comments on most of the papers presented at the symposium.

The first group of papers, dealing with the generation and testing of random numbers and the more general random variables, includes: Generation of Pseudo Random Numbers (Olga Taussky and John Todd); Phase Shifts—Middle Squares—Wave Equation (N. Metropolis); A Description of the Generation and Testing of a Set of Random Normal Deviates (E. J. Lytle, Jr.); and Machine Sampling from Given Probability Distributions (James W. Butler).

Papers in the second group deal primarily with theoretical aspects of Monte Carlo Methods, particularly with the problem of variance reduction. They are: A General Theory of Stochastic Estimates of the Neumann Series for the Solution of Certain Fredholm Integral Equations (G. E. Albert); Neighbor Sets for Random Walks and Difference Equations (Theodore S. Motzkin); Conditional Monte Carlo for Normal Samples (Hale F. Trotter and John W. Tukey); Application of Multiple Stage Sampling Precedures to Monte Carlo Problems (A. W. Marshall); Questionable Usefulness of Variance for Measuring Estimate Accuracy in Monte Carlo Importance Sampling Problems (John E. Walsh); Use of Different Monte Carlo Sampling Techniques (Herman Kahn); A Theoretical

Comparison of the Efficiencies of Two Classical Methods and a Monte Carlo Method for Computing One Component of the Solution of a Set of Linear Algebraic Equations (J. H. Curtiss); and A Monte Carlo Technique for Obtaining Tests and Confidence Intervals for Insurance Mortality Rates (John E. Walsh).

The third group of papers, devoted to the application of the Monte Carlo Methods, contains: Monte Carlo Computations (Nancy M. Dismuke); Monte Carlo Techniques in a Complex Problem about Normal Samples (Harvey J. Arnold, Bradley D. Bucher, Hale F. Trotter, and John W. Tukey); An Application of the Monte Carlo Method to a Problem in Gamma Ray Diffusion (Martin J. Berger); Experimental Determination of Eigenvalues and Dynamic Influence Coefficients for Complex Structures such as Airplanes (C. W. Vichery) (abstract only); and Application of Monte Carlo Methods to Tactical Games (S. Ulman) (abstract only).

The last paper in the book, by Alvin Walther, on Experiments and Models for the Monte Carlo Method, describes a simple experiment in the Technische Hochschule at Darmstadt in which the Monte Carlo Method was used to evaluate a definite integral.

Part II of the book (87 pages) contains a bibliography of papers related to the Monte Carlo Method which appeared during the years 1949–1954. Since the papers are not readily accessible, abstracts of most of them are included. The bibliography is grouped as follows: Monte Carlo Proper (Part I); The Generation and Testing of Random Digits and Known Sources of Random Digit Tables (Part II); Articles and Books, Mostly Without Abstracts, in which Sampling is Primarily Relied Upon for a Solution or Verification (Part III); A Selection of Articles and Books on, or Making Use of, Stochastic Processes, Including Extracts from a Bibliography Supplied by D. G. Kendall, Mostly without Abstracts (Part IV).

This book is undoubtedly for the expert, as a high degree of mathematical sophistication and a good understanding of mathematical statistics are essential in order to comprehend most of the papers. Readers who have this background will find the book very interesting and stimulating. For persons interested in applying the Monte Carlo Method on electronic computers, the book is an important guide and reference.

ELIEZER NADDOR

DE OMNIBUS REBUS ET QUIBUSDAM ALIIS

WHAT IS SCIENCE? *Twelve Eminent Scientists and Philosophers Explain Their Various Fields to the Layman.*

Edited by James R. Newman. Simon & Schuster, New York. $4.95. viii + 493 pp.; ill. 1955.

"It is to progress in the human sciences that we must look to undo the evils which have resulted from a knowledge of the physical world hastily and superficially acquired by populations unconscious of the changes in themselves which the new knowledge has made imperative." This, the opening sentence of the concluding paragraph of Bertrand Russell's essay, Science and Human Life, expresses a thought common to most of the twelve essays collected by James R. Newman under the title, *What is Science?*

Each of these essays is written by a scientist of eminence in his field who regards with some optimism the general implications of progress in his special field. Most biologists are familiar with the general views of Ernest Baldwin, Clyde Warder Allee, and Julian Huxley. But they might well be interested in the ways in which pursuit of other disciplines, from cosmology to the study of thinking machines, has contributed to the similar positive philosophies of Sir Edmund Whittaker, Hermann Bondi, Edwin U. Condon, John Read, Edwin G. Boring, Clyde Kluckhohn, Eric Fromm, and Jacob Bronowski. Or, the individuality of each man's thought may be even more revealing. Each has indicated, from his special viewpoint, a portion of the road that may be followed through the best use of man's best tool, his mind.

These essays are written for the intelligent layman. The writing, which varies in degree of lucidity, is always readable, though careful reading is sometimes requisite to following the lines of argument in less familiar fields. Often the reader will find that his personal disagreement with one essay is amplified elsewhere. Both the material and the presentation are thoughtful rather than argumentative. Each chapter is preceded by a short professional and personal biography of the author and is provided with an annotated bibliography at the back of the book for those whose curiosity seeks further non-technical reading in the field.

Biologists with similar philosophical leanings may find that these essays afford a footbridge to their colleagues in other sciences, as well as to their non-scientist friends. Only by circulation can the book fulfill the hope of the editor that it will "help to counteract the malicious doctrines, flourishing again in this age of insecurity, which belittle science and reason."

E. L. WHITE

MAN-MADE FIBER PROGRESS. *Ann. N. Y. Acad. Sci., Vol. 67, Art. 11.*

Edited by Otto v. St. Whitelock. The New York Academy of Sciences, New York. $3.00 (paper). Pp. 897–982; ill. 1957.

THE QUARTERLY REVIEW OF BIOLOGY publishes critical reviews of recent researches in all of the special fields of biological science. The contribution should present a synthesis or digest of the researches and a critical evaluation of them. A mere synopsis of the literature without evaluation or synthesis is not desirable.

Theoretical papers are published occasionally, especially when such papers (1) include a critical synthesis of the literature bearing on the theory and (2) are likely to promote further research in a given field.

The article should be written in concise language, yet in sufficiently non-technical form as to be intelligible not only to specialists in other fields but to the general biologist as well. To this end the article should have a general introduction and a summary which enumerates one by one all of the principal facts and conclusions given in the paper. Interpretative diagrams and schemes are very desirable.

Material ordinarily taking the form of footnotes is set in small print and placed in the text and consequently should be written in a style so as to fit readily into the text. Acknowledgments are printed in the text in small type at the end of the article just preceding the List of Literature. Recent issues of the Quarterly should be examined for style as regards (1) section or subsection headings in the text, (2) literature citations in the text, and (3) List of Literature.

The subjects and authors of articles are selected by the Editors and members of the Advisory Board. Unsolicited articles which conform with the objectives of the Quarterly will be considered for publication.

A feature of the REVIEW is the section dealing with *New Biological Books*. In this department the book literature of different countries in the field of Biology is given comprehensive and critical attention.

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Books for Review may be sent to Dr. H. B. Glass, Department of Biology, The Johns Hopkins University, Baltimore 18, Maryland.

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